Modelización de hábitats y poblaciones para la conservación de las aves marinas

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Habitat and population modelling for the conservation of seabirds

Tesis doctoral - PhD

Andrés de la Cruz Muñoz

2021

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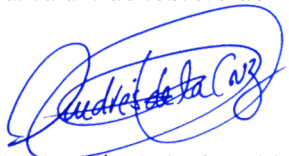
Habitat and population modelling for the conservation of seabirds

Memoria presentada por el doctorando Licenciado en Biología por la Universidad de Sevilla y Máster en Gestión Integrada de Áreas Litorales por la Universidad de Cádiz

Andrés de la Cruz Muñoz

para optar al título de Doctor por la Universidad de Cádiz dentro del Programa de Doctorado Gestión y Conservación del Mar bajo la línea de Conservación y Gestión de Especies y Hábitats de la Escuela Internacional de Doctorado de Estudios Marinos (EIDEMAR), adscrita al Campus de Excelencia Internacional del Mar (CEIMAR), con Mención Internacional.

En Tarifa a 4 de febrero de 2021



Fdo.: Andrés de la Cruz Muñoz

INFORME DEL DIRECTOR

El doctor **Gonzalo Muñoz Arroyo**, profesor contratado doctor de la Universidad de Cádiz, tutor y director de la tesis de **D. Andrés de la Cruz Muñoz**, alumno del programa de doctorado Gestión y Conservación del Mar, regulado por el UCA/CG06/2012, de 27 de junio de 2012, de las enseñanzas oficiales de doctorado de la Universidad de Cádiz,

CERTIFICA:

Que la presente memoria titulada **Modelización de hábitats y poblaciones para la conservación de las aves marinas** - ***Habitat and population modelling for the conservation of seabirds***, presentada por D. Andrés de la Cruz Muñoz para optar al título de Doctor en Gestión y Conservación del Mar con mención internacional ha sido realizada bajo su dirección y tutorización. Esta memoria ha sido desarrollada de acuerdo con los requisitos de control de calidad para las tesis doctorales recogidos en el reglamento UCA/CG06/2012, de 27 de junio de 2012 y sus posteriores modificaciones y autorizo su depósito para su valoración por la Comisión Académica del Programa de Doctorado.

En Puerto Real, a 4 de febrero de 2021

Fdo.: Gonzalo Muñoz Arroyo

ESTRUCTURA Y ORGANIZACIÓN DE LA TESIS DOCTORAL

La tesis doctoral de D. Andrés de la Cruz titulada **Modelización de hábitats y poblaciones para la conservación de las aves marinas - *Habitat and population modelling for the conservation of seabirds*** cuenta con cuatro capítulos, de los cuales, dos han sido publicados como artículos científicos y los otros dos capítulos se encuentran en revisión para su publicación, todos en revistas pertenecientes al JCR (*Journal Impact Factor*), a saber:

- Capítulo 1. How adequately are the critically endangered Balearic shearwaters protected by the Special Protection Areas (SPAs) for seabirds? A case study in the Gulf of Cadiz. Arroyo, G.M., **De la Cruz, A**. y Delgado, D., (2020). Global Ecology and Conservation 21, e00861.
Doi 10.1016/j.gecco.2019.e00861
Factor de impacto (2019): 2.526.
Q2 en la categoría de *Biodiversity Conservation*
Q2 en la categoría de *Ecology*

- Capítulo 2. Drivers for spatial modelling of a critically endangered seabird on a dynamic ocean area: Balearic shearwaters are non-vegetarian.
De la Cruz, A., Ramos, F., Navarro, G., Cózar, A., Bécares, J. y Arroyo, G.M. (2021). Aquatic Conservation: Marine and Freshwater Ecosystems.
Doi 10.1002/aqc.3542
Factor de impacto (2019): 2.572.
Q1 en la categoría de *Marine & Freshwater Biology*
Q2 en la categoría de *Environmental Sciences*
Q2 en la categoría de *Water Resources*

- Capítulo 3. Predator-prey relationship reveals seabirds' spatial distribution in the Gulf of Cadiz.
De la Cruz, A., Ramos, F., Navarro, G., Tornero, J., Jiménez, M.P., Rincón, M., y Arroyo, G.M.
En revisión en ICES Journal of Marine Science.

Factor de impacto (2019): 3.188.
Q1 en la categoría de *Marine & Freshwater Biology*
Q1 en la categoría de *Oceanography*
Q1 en la categoría de *Fisheries*

- Capítulo 4. What to expect from alternative management strategies to conserve seabirds? Hints from a dynamic modelling framework applied to an endangered population.
De la Cruz, A., Bastos, R., Silva, E., Cabral, J.A. y Santos, M.
En revisión en Animal Conservation.
Factor de impacto (2019): 3.210.
Q1 en la categoría de *Biodiversity Conservation*
Q2 en la categoría de *Ecology*

La contribución de Andrés de la Cruz en los capítulos indicados ha sido: diseño y conceptualización del estudio, toma y recogida de datos, análisis de datos, redacción del manuscrito, edición y visualización.

El director certifica que los artículos científicos citados anteriormente y que conforman la presente tesis doctoral no han sido utilizados, implícita o explícitamente, para la realización de otras tesis doctorales.

En Puerto Real, a 4 de febrero de 2021

Fdo.: Gonzalo Muñoz Arroyo

A mis padres,
por su apoyo incondicional, por su cariño

Cita recomendada de la tesis:

De la Cruz, A. (2021). Modelización de hábitats y poblaciones para la conservación de las aves marinas - *Habitat and population modelling for the conservation of seabirds*. Tesis Doctoral - PhD Thesis. Universidad de Cádiz.

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RESUMEN

ABSTRACT

RESUMEN

La presente tesis doctoral pretende avanzar en el conocimiento sobre la ecología de las de aves marinas en relación a su distribución espacial y sus tendencias poblacionales en el ámbito de las áreas marinas protegidas. Los resultados y conclusiones obtenidos en los trabajos que componen esta tesis buscan aportar nueva información y soluciones reales que mejoren el estado de conservación del mar a la vez que aspiran a ser herramientas prácticas que puedan ser utilizadas por gestores o investigadores en la toma de decisiones para la protección, conservación y gestión del medio marino.

Para ello, en el desarrollo de los diferentes capítulos de este trabajo se han aplicado diferentes técnicas de modelado espacial (análisis de densidad Kernel y diversos modelos generalizados) y análisis demográficos (modelos de dinámica de sistemas) a una serie temporal de datos de especies indicadoras del medio, las aves marinas. Los trabajos se han realizado en el marco de dos áreas marinas protegidas: la Zonas de Especial Protección para las Aves (ZEPA) Área Marina del Golfo de Cádiz y la ZEPA Área Marina del Archipiélago de las Berlengas.

Los resultados obtenidos muestran que el área clave para la pardela balear en el Golfo de Cádiz se localiza en aguas poco profundas entre la desembocadura del Guadalquivir y la zona marina frente a la Bahía de Cádiz y que la delimitación de la actual ZEPA cubre menos del 40% de dicha área clave. Ante estos resultados, se hace necesario extender esta área marina protegida hacia el sureste de su posición actual para cubrir toda la superficie clave identificada para la especie. Además, los resultados ponen de manifiesto la necesidad de utilizar datos robustos procedentes de series temporales largas para delimitar áreas marinas protegidas de manera consistente.

En el segundo capítulo se demuestra que las variables abióticas, como la batimetría o la distancia al Guadalquivir, han resultado ser mejores predictores del hábitat esencial de la pardela balear frente a factores bióticos, como la concentración de clorofila. Estos resultados difieren de los encontrados por otros autores en otras áreas de distribución de la especie y nos indican que, en ambientes oceánicos altamente dinámicos, el desfase espacio-temporal entre la producción primaria y los consumidores puede alterar las previsibles relaciones directas.

En el tercer capítulo se relaciona la distribución de las principales especies de aves marinas en el Golfo de Cádiz con el alimento que consumen. Los resultados de los mejores modelos indican que, para las principales especies, la distribución de las aves

marinas está correlacionada y altamente solapada con la de sus presas naturales, peces pequeños pelágicos. Particularmente, la distribución de especies prioritarias, como la pardela balear, se encuentra determinada en el Golfo de Cádiz por la presencia de boquerón y sardina de talla mediana. Otras especies no muestran estas correlaciones, lo que podría indicar que explotan recursos distintos a las especies presa estudiadas.

Finalmente, en el último capítulo de esta tesis doctoral se ha demostrado como la aplicación de modelos de dinámica de sistemas a la población de cormorán moñudo en la ZEPA de las Islas Berlengas ofrece una herramienta muy eficaz en la toma de decisiones en la gestión de las áreas marinas protegidas. En este sentido, las simulaciones señalan a las especies invasoras como las ratas y la mortalidad asociada a la captura accidental por la actividad pesquera como las principales amenazas del cormorán moñudo. Sin aplicar ninguna medida de gestión, la población de cormorán moñudo descendería un 7% en las Islas Berlengas en la próxima década. Sin embargo, esta población relicta podría aumentar notablemente si se mantiene el archipiélago libre de carnívoros invasores y se aplican medidas de mitigación para reducir la muerte de cormorán moñudo por *bycatch*.

En las diferentes investigaciones llevadas a cabo en esta tesis doctoral se demuestra la utilidad de la aplicación de modelos estadísticos al estudio de especies de depredadores marinos indicadoras del medio. En este caso, la conservación de las aves marinas y las áreas marinas protegidas del ámbito de estudio son esenciales para una eficaz protección y gestión del ecosistema marino. Prueba de ello es la reciente propuesta de ampliación de la ZEPA Área Marina del Golfo de Cádiz, basada en los resultados de esta tesis doctoral, que ha sido aceptada por el Ministerio para la Transición Ecológica y el Reto Demográfico en el marco del proyecto LIFE-IP INTEMARES.

ABSTRACT

This PhD thesis aims to advance the knowledge about the ecology of seabird species in relation to their spatial distribution and their population trends within the framework of the marine protected areas. The results and conclusions obtained in this study seek to provide new information and real solutions to improve the conservation status of the sea. At the same time, they aspire to be practical tools that can be used by managers or researchers in making decisions concerning the protection, conservation and management of the marine environment.

To this end, different spatial modelling techniques (kernel density analysis and generalised models) and demographic analysis (system dynamics models) have been applied to a long-term data series of bioindicator species of the marine environment (seabirds) within the framework of two marine protected areas: The Special Protection Area for Birds (SPA) Marine Area of the Gulf of Cádiz (Spain) and the Marine Area of the Berlengas Archipelago (Portugal).

The results obtained show that the key area for the Balearic shearwater in the Gulf of Cádiz is located in shallow waters between the mouth of the Guadalquivir River and the marine area located off the Bay of Cádiz, and therefore, the delimitation of the current SPA covers less than 40% of this key area. Against this background, it is necessary to extend this marine protected area to the southeast of its current position to cover the entire key area identified for the species. In addition, the results highlight the need to use robust data over a long time period to consistently identify marine protected areas.

In the second chapter, it is shown that abiotic variables, such as bathymetry or the distance to the Guadalquivir River, have turned out to be better predictors of the essential habitat of the Balearic shearwater compared to biotic factors, such as chlorophyll concentration. These results differ from those found by other authors in other areas of the species and indicate that in highly dynamic oceanic environments the spatio-temporal lag between primary production and consumers can alter the foreseeable direct relationships.

In the third chapter, the distribution of the main species of seabirds in the Gulf of Cádiz is related to the food they consume. The results of the best models indicate that, for the main species, the distribution of seabirds is correlated and highly overlapped with that of small pelagic fish, their natural prey. In particular, the distribution of priority species, such as

the Balearic shearwater, is determined by the presence of medium-sized anchovies and sardines in the Gulf of Cádiz. Other species do not show these correlations, which could indicate that they exploit other resources than the prey species studied.

In the last chapter, it is demonstrated how the application of systems dynamics models to the Shag population in the Berlengas Archipelago SPA offers a very effective decision-making tool in the management of marine protected areas. In this sense, the simulations indicate invasive species such as rats and mortality associated with accidental capture due to fishing activity as the main threats to the Shag. Without applying any management measures, Shag population would decline by 7% in the Berlengas Islands in the next decade. However, this relict population could increase significantly if the archipelago is kept free of invasive carnivores and mitigation measures are applied to reduce *bycatch*.

In the research carried out for this thesis, the usefulness of applying statistical models to the study of marine predator species as ecological indicators is demonstrated. In this case, the conservation of seabirds and the marine protected areas in the study area are essential for effective conservation and management of the marine ecosystem. Proof of this is the recent proposal to expand the Marine Area of the Gulf of Cádiz SPA, based on the results of this doctoral thesis, which has been accepted by the Ministry for the Ecological Transition and the Demographic Challenge within the framework of the LIFE-IP INTEMARES project.

INTRODUCCIÓN GENERAL

Los cambios en la biodiversidad del medio marino: una visión desde un enfoque ecosistémico

Los mares y océanos albergan gran parte de la diversidad del planeta, contando con más de 230.000 especies distintas (WoRMS Editorial Board, 2020). Sin embargo, en su gran mayoría, los océanos se encuentran escasamente protegidos, con tan sólo el 7.6% de su superficie bajo alguna figura de protección (UNEP-WCMC IUCN & NGS, 2021). Esta falta de protección afecta particularmente a las zonas pelágicas alejadas de la costa, donde aplicar eficaces planes de gestión implica retos aún no resueltos (Luypaert *et al*., 2019).

Cada vez hay más evidencias de que la biodiversidad de los ecosistemas marinos está cambiando en respuesta a la alteración del clima y la actividad humana. Son muchas las acciones llevadas a cabo por el hombre y desarrolladas en el mar que provocan un impacto negativo en el medio. Estas acciones se traducen en un declive poblacional de las especies marinas debido principalmente a la reducción o empeoramiento de su hábitat o mediante la reducción de los propios individuos (Hammerschlag *et al*., 2019; Doney *et al*., 2020). Ante esta situación, muchos organismos han visto alterado su hábitat natural, debiendo modificar su comportamiento para poder adaptarse a tales cambios. Numerosos estudios demuestran como causante de estas alteraciones a las actividades humanas desarrolladas en el mar, que provocan pérdida de hábitat, contaminación, sobreexplotación de recursos, propagación de enfermedades, ruido o incluso molestias provocadas por el turismo, forzando a estas especies a cambiar sus zonas de alimentación o reproducción, incrementando consecuentemente sus tasas de mortalidad, reduciendo su éxito en la búsqueda de alimento o empeorando su condición física (Fink, 2017; Simmonds, 2017; Mendel *et al*., 2019; Healy *et al*., 2020; Wildermann *et al*., 2020). Por desgracia, no todos los organismos consiguen adaptarse favorablemente y, consecuentemente, muchos de estos taxones se encuentran gravemente amenazados o, en algunos casos, se han extinguido (Di Marco *et al*., 2018; Wilson *et al*., 2020).

Ante esta situación, el estudio de la distribución y la dinámica de las poblaciones de los organismos marinos pueden reflejar tales cambios y ofrecernos las herramientas necesarias para predecir potenciales cambios negativos y, tras ello, actuar en consecuencia (Zhang *et al*., 2017; Canonico *et al*., 2019; Griffith, 2020). Además, ante la complejidad y dinamismo del medio marino, es necesario aplicar a estos estudios un enfoque ecosistémico, centrado en entender los procesos que subyacen tras el comportamiento, la distribución –espacial y tem-

poral– y la dinámica poblacional de las especies estudiadas, frente a otros enfoques parciales o que sólo buscan relaciones no necesariamente causales. Para ello, es necesario aplicar metodologías científicas adecuadas centradas en comprender las relaciones, funciones e interacciones esenciales entre los organismos y su entorno, incluyéndonos a los seres humanos (Ressurreição *et al*., 2012). En este sentido, los grandes depredadores marinos –cetáceos, pinnípedos, tortugas, aves y peces– son sin duda uno de los grupos idóneos sobre los que basar este tipo de estudios, puesto que son elementos icónicos del ecosistema oceánico, que desempeñan un papel fundamental en el sistema como grandes consumidores, estructurando y conectando las complejas redes tróficas marinas (Bestley *et al*., 2020).

Los modelos matemáticos: una aproximación para afrontar la crisis de la biodiversidad marina

Ante esta crisis de biodiversidad marina, diferentes herramientas han sido ampliamente desarrolladas para tratar de comprender los procesos y relaciones que se dan en los ecosistemas marinos con el objetivo de dar respuesta a sus problemas de conservación. Una de las herramientas más utilizadas para explicar los fenómenos que se producen en el mar y tratar de predecir las alteraciones y sus posibles consecuencias en un marco espacio-temporal son los modelos matemáticos y, entre ellos, los modelos estadísticos o probabilísticos. Estos modelos no son más que diferentes fórmulas matemáticas aplicadas para comprender de manera simplificada la realidad que observamos en el medio. En otros casos, estos modelos ayudan a explicar las causas y a predecir el sentido y la magnitud de los cambios que pueden producirse en la biodiversidad marina ante distintos escenarios. De esta forma, podemos estudiar de manera controlada el comportamiento de un sistema complejo y dinámico como el medio marino (Fulton *et al*., 2015).

Entre los modelos más utilizados en el estudio del ecosistema marino encontramos los modelos de distribución espacial o modelos de hábitat esencial y los modelos de viabilidad poblacional, como son los modelos demográficos (McDonald *et al*., 2008; Grémillet & Boulinier, 2009; Beltran *et al*., 2017; García-Barón *et al*., 2019).

Los modelos de distribución de especies se utilizan sistemáticamente para comprender y predecir el patrón de distribución de la biodiversidad. Estos modelos se basan en determinar la relación entre la ocurrencia de las especies a estudiar y las características

ambientales del lugar donde se encuentran (Franklin, 2010), lo cual proporciona información fundamental sobre las causas por las que encontramos o no, diferentes especies marinas en determinadas zonas. Estos modelos de distribución se han consolidado en los últimos años como una herramienta clave en la investigación de la ecología y la biogeografía marina (Reisinger *et al*., 2018; Fernandes *et al*., 2019), llegando a ser esenciales en la identificación de áreas importantes y prioritarias para la conservación de especies (Sánchez-Carnero *et al*., 2016). Tras la identificación de estas áreas clave, administradores y gestores pueden reducir los posibles conflictos o impactos mediante una eficaz gestión y ordenación de las actividades a desarrollar en estos espacios prioritarios. Estos modelos de distribución de especies se han utilizado en cientos de artículos para predecir el rango geográfico actual y futuro del nicho ambiental de los depredadores marinos (Robinson *et al*., 2017). Además, numerosos trabajos modelizan el cambio de la distribución de estas especies para dar la voz de alarma ante cambios negativos en el ecosistema, tales como deterioro del hábitat, sobreexplotación o contaminación, entre otros (p.ej., Catry *et al*., 2013; Hazen *et al*., 2017; C. Lambert *et al*., 2017c).

Por otro lado, los modelos demográficos se han utilizado particularmente para el estudio de la dinámica poblacional de especies marinas, ya que permiten predecir la viabilidad de estas especies a largo plazo y evaluar los riesgos de extinción de especies amenazadas (Morris & Doak, 2002). Una de las metodologías más aceptadas y útiles en la predicción del éxito de supervivencia de una especie son los modelos dinámicos, que incorporan toda la información biológica disponible de la especie a estudiar (Anderson *et al*., 2018; Miller *et al*., 2019). De hecho, el modelado dinámico se considera actualmente una herramienta fundamental en ecología, al fusionar información dispersa dentro de un marco común, permitiendo además predecir las consecuencias futuras de escenarios alternativos de manejo (Weller *et al*., 2016). Entre las diferentes aproximaciones para aplicar estos modelos, la dinámica de sistemas (*system dynamics*) se ha considerado particularmente útil por optimizar las estrategias de gestión y las medidas que ayudan a la toma de decisiones (Santos *et al*., 2013).

Muchos trabajos elaboran modelos predictivos gracias a la utilización de dinámica de sistemas donde la extinción de las especies marinas sería una realidad en las próximas décadas si no se aplican acciones de conservación eficaces (Davidson *et al*., 2012; Genovart *et al*., 2016; Anderson *et al*., 2018). En estos casos, gracias a los resultados que muestran

los diferentes escenarios de estos modelos dinámicos, el modelador puede probar rápida y reversiblemente lo que sucede bajo diferentes acciones de manejo. En consecuencia, los modelos pueden ayudarnos a responder preguntas sobre la conservación e incluso sobre potenciales resultados socio-económicos tras la ejecución las actuaciones propuestas (Santos *et al*., 2016).

Sin embargo, debemos tener presente que ningún modelo estadístico aplicado a procesos ecológicos conseguirá explicar o predecir la totalidad de las interacciones y relaciones que en el medio se producen. Si bien es cierto que, en las últimas décadas, gracias al aumento de la capacidad computacional, el contenido y la complejidad de los modelos utilizados en la conservación del medio marino ha crecido notablemente (Fulton *et al*., 2015), no debemos olvidar que la obtención de un modelo bueno o aceptable depende en gran medida del conocimiento y las técnicas concretas aplicadas a la hora de discernir entre cual es y cual no, el mejor modelo obtenido. En muchos casos, sutiles cambios en la elección de estas técnicas nos ofrecerán resultados diferentes (Guisan & Zimmermann, 2000; Radosavljevic & Anderson, 2014). Como consecuencia, muchos autores apoyan el uso de distintos tipos de modelos e incluso la combinación entre sí para obtener una mejor explicación o predicción general (Araujo & New, 2007; Oppel *et al*., 2012).

Por otro lado, uno de los factores fundamentales que determina la precisión de las predicciones de un modelo es la calidad (y, por ende, la cantidad) de los datos que lo nutren. En el mar, uno de los principales problemas a los que se enfrenta la conservación del medio natural es la escasez de series largas de datos (Hughes *et al*., 2017). Estos datos recogidos a lo largo de sucesivas campañas son muy necesarios para entender correctamente la dinámica poblacional, conocer el riesgo de extinción o identificar el hábitat esencial de una especie (White, 2019). Ante esta situación, es necesario elaborar modelos que se nutran de series largas de datos (Braunisch & Suchant, 2010; García-Barón *et al*., 2020), donde se incorpore una parte importante de la variabilidad temporal. Este aumento en el número de años de muestreo permite elaborar modelos más robustos que ofrezcan resultados más fiables y sólidos (Brotons *et al*., 2007; Meynard *et al*., 2019).

Por último, y con el objetivo de obtener modelos explicativos o predictivos bajo un enfoque ecosistémico, es necesario considerar el mayor número de elementos del ecosistema marino que nos permita analizar el conjunto del sistema. Ante este tipo de modelos, se

requiere dar un paso más y obtener información sobre las relaciones de las distintas especies del medio marino, destacando entre estas interacciones, las relaciones tróficas depredador-presa para lograr una correcta parametrización y evaluación del propio modelo y comprender así qué papel juegan los diferentes eslabones de esta cadena (Fulton *et al*., 2015; Astarloa *et al*., 2019).

Las aves marinas como indicadores del medio y su estado de conservación

Existe una base amplia de conocimiento que demuestra que las aves marinas son excelentes indicadores del estado de los mares y océanos (Piatt & Sydeman, 2007; Rajpar *et al*., 2018). Su presencia en casi todos los ambientes marinos, sus amplios movimientos que cubren grandes áreas del océano y los cambios en su distribución integran alteraciones que ocurren en diferentes niveles, tanto espacial como temporal (Schreiber & Burger, 2001). Además, las aves marinas funcionan como depredadores apicales en el ecosistema marino, situándose en los niveles más altos de la red trófica estructurando dicha red y, por tanto, son sensibles a los cambios que se producen en todos los eslabones de la cadena alimentaria marina (Hazen *et al*., 2019). Por otro lado, gracias a que las aves marinas son relativamente grandes y conspicuas, son fáciles de monitorear y su estudio ha servido para evaluar el estado de salud de diferentes ambientes marinos, al proporcionar la información necesaria para detectar cambios ante impactos como fuentes de contaminantes, alteración de las poblaciones de peces o eventos climáticos y oceanográficos (Furness & Camphuysen, 1997; Provencher *et al*., 2019).

Todas estas características definen buena parte de la bio-ecología de las aves marinas, haciendo a este grupo un buen indicador del ecosistema marino y, por ello, las aves marinas son consideradas como unas excelentes centinelas del mar (Piatt & Sydeman, 2007). Sin embargo, muchas de las razones por las que las aves marinas son un buen termómetro ecológico, son también las responsables de los problemas de conservación a las que se enfrentan. Su vínculo al mar y a la tierra firme, su baja tasa de reproducción junto a su madurez sexual tardía y las enormes áreas que cubren en sus desplazamientos, hacen que las aves marinas sumen diferentes amenazas que empeoran su estado de conservación. Esto ha provocado que actualmente las aves marinas sean uno de los grupos de aves más amenazados a nivel mundial (Dias *et al*., 2019) con descensos en las poblaciones monitoreadas de casi un 70% en los últimos 60 años (Paleczny *et al*., 2015).

Entre las amenazas más importantes que afectan a este grupo de aves, destacan la pérdida de hábitat adecuado para su reproducción, la rápida disminución de sus poblaciones de presas –debido principalmente a la sobrepesca y la contaminación del agua– (Croxall *et al*., 2012; Dias *et al*., 2019), el efecto de especies exóticas invasoras (Spatz *et al*., 2017) o la mortalidad producida por la captura accidental de aves marinas en diferentes artes de pesca o *bycatch* (Clay *et al*., 2019). Estas amenazas, unidas a los cambios en el medio marino producido por el aumento de las temperaturas a escala global, afectan a tres cuartas partes de las especies de aves marinas y a casi 400 millones de individuos (Dias *et al*., 2019). Actualmente, casi un 30% de las especies se encuentran amenazadas globalmente y un 14% del total de especies se encuentra en riesgo de desaparecer bajo las categorías de 'En peligro' o 'En peligro crítico' de extinción (Dias *et al*., 2019) (Figura 1). Ante esta situación, muchas especies de aves marinas necesitan la puesta en marcha de acciones eficaces de conservación que reduzcan o mitiguen las causas que provocan el declive de sus poblaciones.

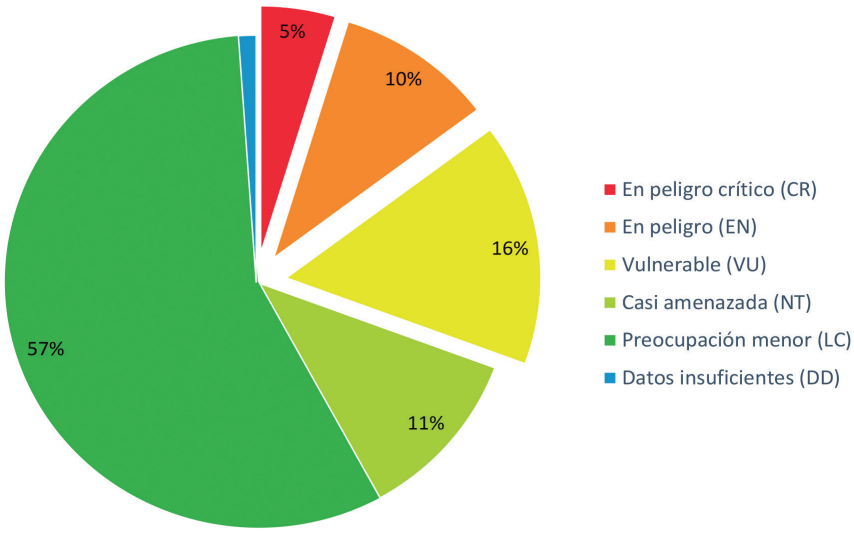


Figura 1. Proporción de especies de aves marinas amenazadas globalmente y sus categorías de amenaza según UICN. Elaboración propia a partir de Dias *et al*., (2019).

Las áreas marinas protegidas: una posible solución, pero, ¿siempre efectiva?

Una de las herramientas más importantes que se han desarrollado en las últimas décadas para conservar el medio marino y por lo tanto a las especies que habitan en él, ha sido la creación de Áreas Marinas Protegidas (AMP). Estas áreas tienen el claro objetivo de conservar la vida en el mar y son una herramienta reconocida mundialmente para gestionar y mejorar los ecosistemas marinos mediante la identificación, delimitación y protección de zonas de importancia medioambiental (Watson *et al*., 2014). En los últimos años, estas AMP han experimentado una expansión considerable cubriendo más de 26 millones de km^2 de los océanos del mundo. Gracias a este avance, recientemente se han alcanzado los compromisos acordados por acuerdos internacionales como el Convenio sobre la Diversidad Biológica (CDB) en el que los países firmantes se comprometían a salvaguardar el futuro de sus mares y océanos, «Para 2020 [...] el 10% de las áreas costeras y marinas, especialmente las áreas de particular importancia para la diversidad biológica y servicios ecosistémicos, se conservarán mediante sistemas de áreas protegidas gestionados de manera eficaz y equitativa, ecológicamente representativos y bien conectados junto otras medidas de conservación eficaz e integradas en un amplio paisaje marino [...]» (UNEP-WCMC and IUCN, 2016). Para final de 2016, la Unión Europea ya contaba con el 10.8% de sus aguas marinas bajo la figura de algún AMP, mientras que, en España, gracias a proyectos como INDEMARES (LIFE07 NAT/E/000732) e INTEMARES (LIFE15 IPE/ES/000012), se ha alcanzado finalmente en 2020 una superficie marina protegida del 12%.

Dentro de esta recién actualizada red de conservación del mar, las aves marinas han tenido un papel protagonista gracias a la identificación como AMP de las Áreas Importantes para las Aves y la Biodiversidad (*Important Bird and Biodiversity Area,* IBA). Estas IBA marinas, desarrolladas por BirdLife International (2010), han tenido un papel fundamental en la Unión Europea a la hora de delimitar y designar posteriormente estas zonas importantes para la conservación de la avifauna como ZEPA (Ramírez *et al*., 2017). Estas zonas ZEPA para la conservación de las aves marinas, pasan a formar parte de la Red Natura 2000, la herramienta más importante para la conservación del medio natural en Europa. Sin embargo, la efectividad de las AMP se encuentra actualmente en tela de juicio. Cada vez hay más pruebas que sugieren que en muchas de estas áreas no se aplican realmente estrategias efectivas de protección: muchas de ellas carecen de planes de gestión –en Europa tan sólo el 1,8% (European

Green Party, 2019; WWF, 2019)– o indicadores que permitan evaluar fácilmente el logro de los objetivos propuestos y que determinan, en último caso, la viabilidad de las poblaciones de las especies por las que fueron declaradas. En otros casos, la información de base con la que se delimitaron dichas áreas no fue lo suficientemente precisas, o bien no contaron con el tiempo o los recursos suficientes (Ramírez *et al*., 2017; Claudet, 2018). Ante esta situación y para cumplir verdaderamente su objetivo de proteger la biodiversidad, las AMP debieran ser profundamente revisadas. En muchas áreas protegidas, la falta de seguimiento del ciclo anual de las especies que se concentran en estas zonas no permite conocer las tendencias poblacionales de las mismas (Ramírez *et al*., 2017). Esto conlleva a que se desconozca si actividades potencialmente perjudiciales –como el tráfico marítimo, sobrepesca, capturas accidentales o presión turística, entre otros– afectan y en qué medida a las poblaciones de especies marinas presentes en áreas protegidas. En otros casos, la idoneidad del diseño de las áreas protegidas no ha sido evaluada una vez declaradas (Abecasis *et al*., 2014), por lo que potenciales medidas de gestión no serán eficaces si se aplican en el lugar incorrecto.

Ante esta situación, se hacen necesarios estudios desde un enfoque ecosistémico, capaces de profundizar en el conocimiento de los procesos y relaciones que determinan la distribución y el funcionamiento de las especies marinas entre sí, identificando las relaciones causales existentes entre las especies marinas a conservar con las variables oceanográficas bióticas y abióticas, a diferentes escalas temporales y espaciales. Además, los resultados de estos estudios deberían ser integrados en planes de gestión adaptativos (Hobday *et al*., 2014), ya que los mares y océanos son ambientes particularmente dinámicos donde se predicen importantes alteraciones en las próximas décadas si continúan actuando los impulsores del cambio global (Robinson *et al*., 2017; Coll *et al*., 2020). La falta de estos planes de gestión adaptativos, con un seguimiento de indicadores y plazos que aseguren el cumplimiento de los objetivos por la que se protegieron las áreas clave, junto a medidas para reducir y mitigar los impactos en el ecosistema marino, dificulta tremendamente la ordenación de las actividades que afectan a la biodiversidad, comprometiendo en última instancia, la eficacia de las AMP (Ronconi *et al*., 2012).

OBJETIVOS
HIPÓTESIS

OBJETIVOS E HIPÓTESIS

La protección y conservación de la biodiversidad del medio marino es uno de los aspectos más importantes a los que se enfrentan científicos y gestores en las últimas décadas (Lewison *et al*., 2012). El empeoramiento del estado de salud y conservación del mar, debido principalmente al incremento de las actividades humanas en el ecosistema marino, hace necesario dedicar esfuerzos que minimicen estos impactos. Ante esta situación, la protección y gestión de áreas marinas importantes bajo la figura de Áreas Marinas Protegidas es una de las herramientas más utilizadas actualmente (Provencher *et al*., 2019). No obstante, en muchas ocasiones estas áreas protegidas parecen no cumplir con los objetivos por los que fueron declaradas (Selig & Bruno, 2010; Critchley *et al*., 2018), y las actividades que se desarrollan en ellas podrían comprometer la viabilidad de las poblaciones de aves marinas y otros organismos que habitan esos espacios.

En este sentido, el **objetivo general** de esta tesis doctoral es avanzar en el conocimiento sobre la ecología de especies de aves marinas con respecto a su distribución espacial y sus dinámicas poblacionales en el ámbito de las Áreas Marinas Protegidas. En particular, los trabajos presentados en esta tesis se han centrando en la aplicación de modelos estadísticos para identificar las áreas clave de estas especies y los procesos que subyacen en su distribución y su tendencia poblacional. La consecución de este objetivo nos permitirá determinar la idoneidad de las áreas protegidas para las especies de aves marinas estudiadas por las que fueron declaradas, a la vez que identificar los impactos que amenazan su viabilidad en áreas marinas protegidas de la costa atlántica ibérica.

Los **objetivos específicos** desarrollados en esta tesis doctoral son:

- Identificar el área clave para especies de aves marinas críticamente amenazadas como la pardela balear en el Golfo de Cádiz.
- Identificar y analizar los factores que determinan la distribución espacial de la pardela balear en el Golfo de Cádiz.
- Estudiar las relaciones espaciales entre depredadores apicales (aves marinas) y presas (peces) en el Golfo de Cádiz.
- Modelizar la tendencia poblacional del cormorán moñudo en el archipiélago de las Islas Berlengas bajo diferentes escenarios al aplicar diferentes medidas de gestión.

En este contexto, las **hipótesis** planteadas en esta tesis doctoral han sido:

- La aplicación de modelos espaciales a series temporales de datos de localización de pardela balear en el Golfo de Cádiz permite identificar las áreas clave para la especie, consistentes en el tiempo.
- El área clave para la pardela balear en el área de estudio no se encuentra suficientemente cubierta por la delimitación actual de la ZEPA del Área Marina del Golfo de Cádiz.
- La aplicación de modelos de distribución espacial permite caracterizar el hábitat de la pardela balear en el Golfo de Cádiz, ponderando la importancia relativa de factores bióticos relacionados con la productividad frente a factores abióticos.
- La distribución de los depredadores apicales en ecosistemas marinos altamente dinámicos no se correlaciona con los indicadores de productividad primaria, debido al desacoplamiento espacio-temporal en los procesos a lo largo de las redes tróficas.
- La distribución espacial de depredadores marinos se encuentra determinada, de manera general, por las especies presa sobre las que se alimentan.
- La aplicación de modelos demográficos dinámicos permite predecir la tendencia de la población de cormorán moñudo en la ZEPA Área Marina del Archipiélago de las Berlengas en base a sus principales amenazas y a diferentes escenarios de gestión.

METODOLOGÍA GENERAL

El sistema de estudio: las aves marinas

Existen muchas definiciones de aves marinas, casi todas muy parecidas entre sí y sólo se diferencian en pequeños matices. Sin embargo, todos estaremos de acuerdo si definimos al grupo de las aves marinas como aquellas aves que están ligadas al ambiente marino. Las aves marinas, en general, obtienen su alimento en el mar, descansan en el mar y viajan sobre el mar. Tan sólo están condicionadas a pisar tierra firme durante su período reproductor (Furness & Monaghan, 1986). Esta definición, compartida por muchos autores, siempre pone de manifiesto la vinculación de estas aves al ecosistema marino. Sin embargo, las aves marinas no sólo están condicionadas al mar, sino que viven en hábitats tan distintos como el mar, el aire y tierra firme. Esta capacidad de adaptación a ambientes tan diferentes hace que las aves marinas sean un grupo extraordinario (Schreiber & Burger, 2001). La adaptación de las aves marinas se hace patente cuando encontramos en el mismo grupo aquellas que han perdido su capacidad de volar, como los pingüinos (orden Sphenisciformes), o aves como los albatros, petreles, fulmares o pardelas (orden Procellariiformes), donde muchos vuelan sin parar durante días o semanas en búsqueda de alimento (Croxall *et al*., 2005) o realizan migraciones recorriendo el planeta entero en pocos meses (Newton, 2010). Estos ejemplos nos dan una idea de la tremenda diversidad que podemos encontrar en el grupo de las aves marinas.

Atendiendo a la definición de Croxall *et al*., (2012), las aves marinas son aquellas en las que una proporción de su población depende del medio marino durante al menos parte del año. Así, se establecen 342 especies diferentes, lo que supone un 3.1% de las 10.900 especies de aves catalogadas hasta la fecha (Del Hoyo & Collar, 2014, 2016; Handbook of the Birds of the World and BirdLife International, 2019). Siguiendo una clasificación filogenética clásica, podemos clasificar a las aves marinas en seis órdenes y 12 familias (Tabla 1) (Billerman *et al*., 2020).

Tabla 1. Clasificación de los grupos diferentes de aves marinas en órdenes, familias y nombres comunes según Billerman *et al*., (2020).

Orden	Familia	Nombre común
Sphenisciformes	*Spheniscidae* (6 géneros, 18 especies)	Pingüinos
Procellariiformes	*Diomedeidae* (4 géneros, 15 especies)	Albatros
	Procellariidae (16 géneros, 96 especies)	Pardelas y petreles
	Hydrobatidae (2 géneros, 18 especies)	Paíños
Pelecaniformes	*Pelecanidae* (1 género, 8 especies)	Pelícanos
Suliformes	*Sulidae* (3 géneros, 10 especies)	Alcatraces y piqueros
	Phalacrocoracidae (2 géneros, 40 especies)	Cormoranes
	Fregatidae (1 género, 5 especies)	Fragatas
Phaethontiformes	*Phaethontidae* (1 género, 3 especies)	Rabijuncos
Charadriiformes	*Stercorariidae* (1 género, 7 especies)	Págalos
	Laridae (23 géneros, 97 especies)	Gaviotas y charranes
	Alcidae (11 géneros, 25 especies)	Frailecillos, alcas y araos

Aunque sean muchas y muy diversas las especies que componen este grupo de aves, casi todas comparten ciertas características. De manera general, el tamaño de las aves marinas suele ser mediano-grande, aunque puede variar notablemente. En este grupo encontramos al ave voladora más grande del mundo, el albatros errante *Diomedea exulans,* con 3.5 metros de envergadura alar y de la misma forma encontramos al grupo de los paíños (familia *Hydrobatidae*), que apenas superan los 35 cm de envergadura. Suelen tener un patrón de coloración recurrente, pardo-oscuro por encima y blanco-claro por debajo (Harrison & Fortes, 2003). Su esperanza de vida es larga, se dan casos de albatros que superan los 60 años de edad, manteniendo la capacidad para reproducirse. Siguiendo con aspectos de la reproducción, las aves marinas alcanzan la madurez sexual muy tarde en comparación con otros grupos de aves, algunas aves marinas no consiguen reproducirse hasta su décimo año de vida. Aproximadamente el 95% de las aves marinas crían de manera colonial, variando el tamaño de la colonia desde pocas parejas hasta varios miles de individuos. En estas colonias, el tamaño de la puesta suele ser pequeño y en muchas ocasiones tan sólo ponen un huevo. Por lo tanto, para aumentar las probabilidades de éxito de tan escasa descendencia, las aves marinas dedican un gran esfuerzo a sacar adelante a su prole, dilatando durante meses el cuidado parental (Furness & Monaghan, 1986; Schreiber & Burger, 2001).

Las aves marinas se han diversificado tanto que podemos encontrarlas a lo largo y ancho del planeta, presentes en todos los continentes y en todos los mares. Se alimentan principalmente de peces en el mar, aunque son capaces de comer un gran rango de alimento, desde presas sobre las que depredan, como moluscos o crustáceos, llegando también a depredar sobre pequeños mamíferos u otras aves marinas (Barrett *et al*., 2007). Varias especies de aves marinas muestran un comportamiento cleptoparasitario, al robar el alimento a otras aves o incluso se han especializado con gran éxito en el aprovechamiento de los descartes pesqueros sobre los que carroñean (Depestele *et al*., 2016). Otras especies, como las gaviotas, añaden a su dieta diferentes alimentos como plantas, frutas y semillas (Cramp & Simmons, 1983; Calvino-Cancela, 2011). Muchas de estas especies de gaviotas llegan incluso a adaptarse a buscar su alimento entre la basura que generamos los humanos (Weiser & Powell, 2010).

En la búsqueda de estos alimentos –principalmente peces en el mar–, las aves marinas se desplazan enormes distancias. Encontrar recursos alimenticios para estas aves es todo un desafío: sus presas se distribuyen de manera irregular e inestable y, por lo tanto, son difíciles de predecir y localizar (Bastos *et al*., 2020). Especies de aves marinas como los albatros, pardelas o charranes realizan movimientos migratorios en búsqueda de alimento sobrevolando diferentes mares y océanos, cubriendo decenas de miles de kilómetros (Åkesson & Weimerskirch, 2005; González-Solís *et al*., 2007; Egevang *et al*., 2010). En estos enormes viajes, los patrones globales de circulación oceánica y sus consecuentes *upwellings* o surgencias de aguas profundas cargadas de nutrientes en determinados puntos del planeta son los determinantes en mayor o menor medida de la distribución de las aves marinas (Hunt Jr., 1991). Numerosos trabajos ponen de manifiesto que las aves marinas se concentran allí donde la disponibilidad de alimento es alta (Fauchald, 2009) y, por lo tanto, el estudio de las relaciones entre ambas distribuciones –aves marinas y sus presas– será fundamental para alcanzar un conocimiento apropiado de su ecología. Sin embargo, nos encontramos ante muchas limitaciones a la hora de estudiar estas relaciones. Debido a la inmensidad e inaccesibilidad del océano, el estudio de las distribuciones de las aves marinas está supeditado, en muchas ocasiones, a costosas campañas oceanográficas donde el objetivo principal no es el estudio de las propias aves (Ronconi & Burger, 2009). En otras ocasiones, es necesario realizar el seguimiento de manera remota, mediante el marcaje de tan sólo unos pocos individuos

(Wakefield *et al.*, 2009; Votier *et al.*, 2010), o limitar el estudio a la zona circundante a sus colonias de cría durante el período reproductor (Bolton *et al.*, 2019).

Ámbito de estudio

El ámbito de estudio de los trabajos presentados en esta tesis doctoral se sitúa en el arco atlántico ibérico, es decir, la costa portuguesa y el Golfo de Cádiz. Particularmente, las investigaciones se han focalizado en dos ZEPA marinas: Área Marina del Golfo de Cádiz (ES0000500) en la costa española y Área Marina del Archipiélago de las Islas Berlengas (PTZPE0009) en la costa portuguesa (Figura 2). La extensa plataforma continental nutrida por los sedimentos de grandes ríos es una característica común en estas dos áreas, lo que las convierte en ambientes muy productivos, capaces de albergar a una importante comunidad de especies marinas. Gracias a sus particulares características oceanográficas, ambas zonas cuentan con una gran biodiversidad e importantes caladeros de pesca a nivel nacional e internacional que se traduce en zonas muy antropizadas con un número de actividades humanas muy elevado, que coinciden inevitablemente en el espacio y en el tiempo con las especies

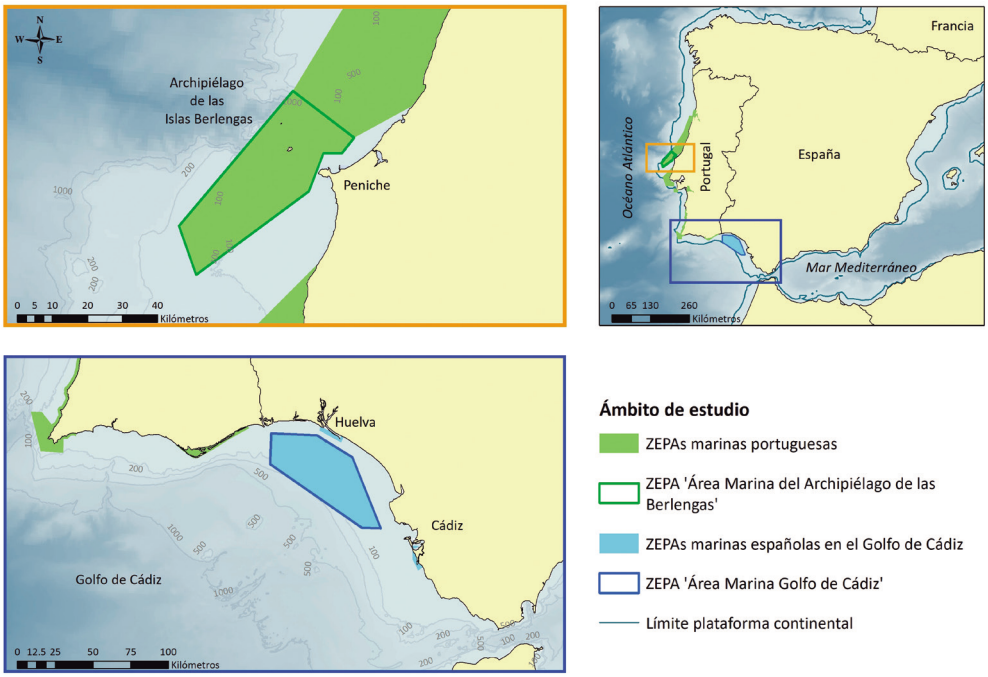


Figura 2 Área de estudio donde se han llevado a cabo los diferentes trabajos incluidos en esta tesis doctoral. Elaboración propia.

marinas. En particular la zona de estudio soporta un alto tráfico marítimo y una importante presión pesquera, actividades que producen algunas de las principales amenazas para los ecosistemas marinos.

Ambas zonas son de gran importancia para las aves marinas, ya que se encuentran dentro de las rutas migratorias de aquellas aves que crían en el Mar del Norte y se desplazan hacia el sur tras su período de cría, a la vez que son utilizadas por especies que crían en el Mediterráneo y salen al océano Atlántico tras reproducirse (De la Cruz, 2013; Alonso *et al*., 2019). Por su parte, el Golfo de Cádiz es la antesala al estrecho de Gibraltar, por lo que será paso obligado para aquellas aves marinas que se desplacen entre el Atlántico y el Mediterráneo (De la Cruz, 2013). Como resultado, las costas atlántica andaluza y portuguesa han sido visitadas por más de 70 especies diferentes de aves marinas en las últimas dos décadas (GBIF.org, 2020). Dentro de este nutrido grupo de especies, aproximadamente unas 50-55 especies son recurrentes cada año en el ámbito de estudio (Ramírez *et al*., 2008; Arcos *et al*., 2009; De la Cruz, 2013; Meirinho *et al*., 2014). Muchas de estas especies frecuentes en la costa atlántica ibérica afrontan serios problemas de conservación y, por ello, se encuentran bajo alguna categoría de amenaza, ya sea bajo criterios internacionales o según criterios nacionales como Libros Rojos de cada país y catálogos nacionales o regionales de fauna amenazada. En la tabla 2, se muestran las especies de aves marinas más representativas del área de estudio junto a su estado de conservación. Como vemos, 12 especies presentan un preocupante estado de conservación para aguas continentales portuguesas y nueve para las aguas del Golfo de Cádiz. De manera global, nueve especies se encuentran amenazadas bajo categorías europeas o globales según criterios de la Unión Internacional para la Conservación de la Naturaleza (UICN). De entre todas las especies presentes en el área de estudio, cabe destacar a la pardela balear *Puffinus mauretanicus*, catalogada con el máximo estado de amenaza en las tres categorías evaluadas. Esta especie, endémica de las Islas Baleares, cuenta actualmente con una población que no supera los 27.000 individuos aproximadamente (Arroyo *et al*., 2016) y a nivel global se encuentra En Peligro Crítico de Extinción (Birdlife International, 2020). Tras su período de reproducción, casi la totalidad de individuos de esta especie sale del Mar Mediterráneo y es frecuente en el área de estudio durante sus movimientos migratorios desde finales del mes de mayo hasta finales de septiembre (Guilford *et al*., 2012).

Otras especies representativas del área de estudio, particularmente en el Golfo de Cádiz, han sido la pardela cenicienta *Calonectris diomedea/borealis*, el alcatraz atlántico *Morus bassanus*, el paíño europeo *Hydrobates pelagicus* y la gaviota de Audouin *Ichthyaetus audouinii*. Las pardelas cenicientas (catalogadas como Vulnerable a nivel nacional) y alcatraces atlánticos han sido las especies más numerosas y ampliamente distribuidas en el área de estudio durante los años analizados, alcanzando los miles de individuos (sin contabilizar a las gaviotas patiamarillas *Larus michahellis* y gaviotas sombrías *Larus fuscus*). Por su parte, la gaviota de Audouin, también Vulnerable tanto en España como Portugal, acude frecuentemente a los descartes de los pesqueros y forma parte de las especies más importantes en la avifauna del Golfo de Cádiz. Por último, el paíño europeo es común y frecuente tras su período reproductor en el Golfo de Cádiz. Además, debido al origen desconocido de estas poblaciones y su poca detectabilidad, lo convierte en una especie de estudio muy interesante (Arcos *et al*., 2009).

Otra de las especies de aves marinas estudiadas en esta tesis ha sido la población portuguesa del cormorán moñudo *Gulosus aristotelis* en el archipiélago de las Islas Berlengas. Esta población, casi relicta en Portugal, está catalogada como Vulnerable en el país luso, supone más del 75% de la población portuguesa y debido a los problemas y presiones a la que está sometida, presenta un preocupante declive poblacional (BirdLife International, 2018a; Pereira & Oliveira, 2019).

El Golfo de Cádiz

De manera particular, el área estudiada en el Golfo de Cádiz incluye toda la franja marina frente a la región del Algarve, en la costa sur de Portugal y la costa suroeste española. El área se extiende desde el cabo de Trafalgar, en la costa española, hasta el cabo de San Vicente en Portugal sobre 390 kilómetros de costa y un área total de aproximadamente 17.500 km^2. Toda esta zona tiene gran importancia para las aves marinas durante el invierno y sus pasos migratorios. Las especies más representativas de este espacio protegido son la pardela cenicienta, alcatraz atlántico, pardela balear, págalo grande *Stercorarius skua* y gaviota de Audouin (Arcos *et al*., 2009; De la Cruz, 2013). A su vez, este espacio alberga otras dos AMP costeras (también catalogadas como ZEPA) importantes para la reproducción de aves marinas como el charrancito común *Sternula albifrons*: Área Marina de Tinto & Odiel (ES0000501) y Área Marina de la Bahía de Cádiz (ES0000502).

Islas Berlengas

El archipiélago de las Berlengas –situado frente a Peniche, en la costa occidental de Portugal– está compuesto por tres islas e islotes (Berlenga Grande, Estelas y Farilhões). Estas islas junto a sus aguas circundantes componen la ZEPA del Área Marina del Archipiélago de las Berlengas, superando las 100.000 ha de aguas protegidas. Este archipiélago es un importante ecosistema marino e insular debido a la ocurrencia de varias especies endémicas de plantas y reptiles, invertebrados marinos, peces y mamíferos marinos. En relación a la avifauna marina, las Islas Berlengas cuentan con importantes poblaciones reproductoras de pardela cenicienta, paíño de Madeira *Oceanodroma castro*, gaviota patiamarilla, gaviota sombría y cormorán moñudo. El área también es importante para especies migratorias como el alcatraz atlántico y la pardela balear (Lecoq, 2003; Meirinho *et al*., 2014).

Tabla 2. Especies más representativas y frecuentes en la avifauna marina del área de estudio, Golfo de Cádiz y costa de Portugal junto a sus categorías de amenaza a nivel nacional en Portugal (Livro Vermelho dos Vertebrados de Portugal) (Cabral *et al*., 2005) y España (Catálogo Nacional de Especies Amenazadas) (BOE, 2011) y categorías europeas según la UICN (IUCN, 2020a). Las especies sombreadas forman parte de las investigaciones llevadas a cabo en esta tesis doctoral.

Nombre científico	Nombre inglés	Nombre español	Livro Vermelho Portugal Continental	Catálogo Nacional (España) de Especies Amenazadas	Categoría Europa IUCN (*Global)
Gavia immer	Common Loon	Colimbo grande			VU
Fulmarus glacialis	Northern Fulmar	Fulmar boreal			EN
Bulweria bulwerii	Bulwer's Petrel	Petrel de Bulwer			LC
Calonectris diomedea	Scopoli's Shearwater	Pardela cenicienta mediterránea		VU	LC
Calonectris borealis	Cory's Shearwater	Pardela cenicienta atlántica	VU		LC
Ardenna gravis	Great Shearwater	Pardela capirotada			LC
Ardenna grisea	Sooty Shearwater	Pardela sombría			NT*
Puffinus puffinus	Manx Shearwater	Pardela pichoneta		VU	LC
Puffinus mauretanicus	Balearic Shearwater	Pardela balear	CR	EN	CR

Tabla 2. (Cont.)

Nombre científico	Nombre inglés	Nombre español	Livro Vermelho Portugal Continental	Catálogo Nacional (España) de Especies Amenazadas	Categoría Europa IUCN (*Global)
Puffinus baroli	Little Shearwater	Pardela chica		VU	NE
Oceanites oceanicus	Wilson's Storm-petrel	Paiño de Wilson			LC*
Hydrobates pelagicus	European Storm-petrel	Paíño europeo			LC
Oceanodroma leucorhoa	Leach's Storm-petrel	Paíño boreal			VU
Oceanodroma monorhis	Swinhoe's Storm-petrel	Paíño de Swinhoe			NT*
Oceanodroma castro	Band-rumped Storm-petrel	Paíño de Madeira	VU	VU	LC*
Phaethon aethereus	Red-billed Tropicbird	Rabijunco etéreo			LC*
Morus bassanus	Northern Gannet	Alcatraz atlántico			LC
Sula leucogaster	Brown Booby	Piquero pardo			LC*
Phalacrocorax carbo	Great Cormorant	Cormorán grande			LC
Gulosus aristotelis	European Shag	Cormorán moñudo	VU	VU	LC
Melanitta nigra	Common Scoter	Negrón común	EN		LC
Melanitta fusca	Velvet scoter	Negrón especulado			VU
Phalaropus lobatus	Red-necked Phalarope	Faloropo picofino			LC
Phalaropus fulicarius	Grey Phalarope	Faloropo picogrueso			LC*
Stercorarius pomarinus	Pomarine Jaeger	Págalo pomarino			LC
Stercorarius parasiticus	Parasitic Jaeger	Págalo parásito			LC
Stercorarius longicaudus	Long-tailed Jaeger	Págalo rabero			LC
Stercorarius skua	Great Skua	Págalo grande			LC
Ichthyaetus melanocephalus	Mediterranean Gull	Gaviota cabecinegra			LC
Chroicocephalus ridibundus	Common Black-headed Gull	Gaviota reidora			LC
Ichthyaetus audouinii	Audouin's Gull	Gaviota de Audouin	VU	VU	LC
Larus delawarensis	Ring-billed Gull	Gaviota de Delaware			LC
Larus canus	Mew Gull	Gaviota cana			LC

Tabla 2. (Cont.)

Nombre científico	Nombre inglés	Nombre español	Livro Vermelho Portugal Continental	Catálogo Nacional (España) de Especies Amenazadas	Categoría Europa IUCN (*Global)
Larus fuscus	Lesser Black-backed Gull	Gaviota sombría	VU/LC		LC
Larus argentatus	Herring Gull	Gaviota argéntea			NT
Larus michahellis	Yellow-legged Gull	Gaviota patiamarilla			LC
Larus hyperboreus	Glaucous Gull	Gavión hiperbóreo			LC
Larus marinus	Great Black-backed Gull	Gavión atlántico			LC
Xema sabini	Sabine's Gull	Gaviota de Sabine			LC
Rissa tridactyla	Black-legged Kittiwake	Gaviota tridáctila			VU
Gelochelidon nilotica	Gull-billed Tern	Pagaza piconegra			LC
Hydroprogne caspia	Caspian Tern	Pagaza piquirroja	EN		LC
Thalasseus sandvicensis	Sandwich Tern	Charrán patinegro	NT		LC
Sterna dougallii	Roseate Tern	Charrán rosado			LC
Sterna hirundo	Common Tern	Charrán común	EN		LC
Sterna paradisaea	Arctic Tern	Charrán ártico			LC
Sternula albifrons	Little Tern	Charrancito común	VU		LC
Chlidonias hybrida	Whiskered Tern	Fumarel cariblanco	CR		LC
Chlidonias niger	Black Tern	Fumarel común		EN	LC
Uria aalge	Common Murre	Arao común	CR/NT		NT
Alca torda	Razorbill	Alca común			NT
Fratercula arctica	Atlantic Puffin	Frailecillo atlántico			EN

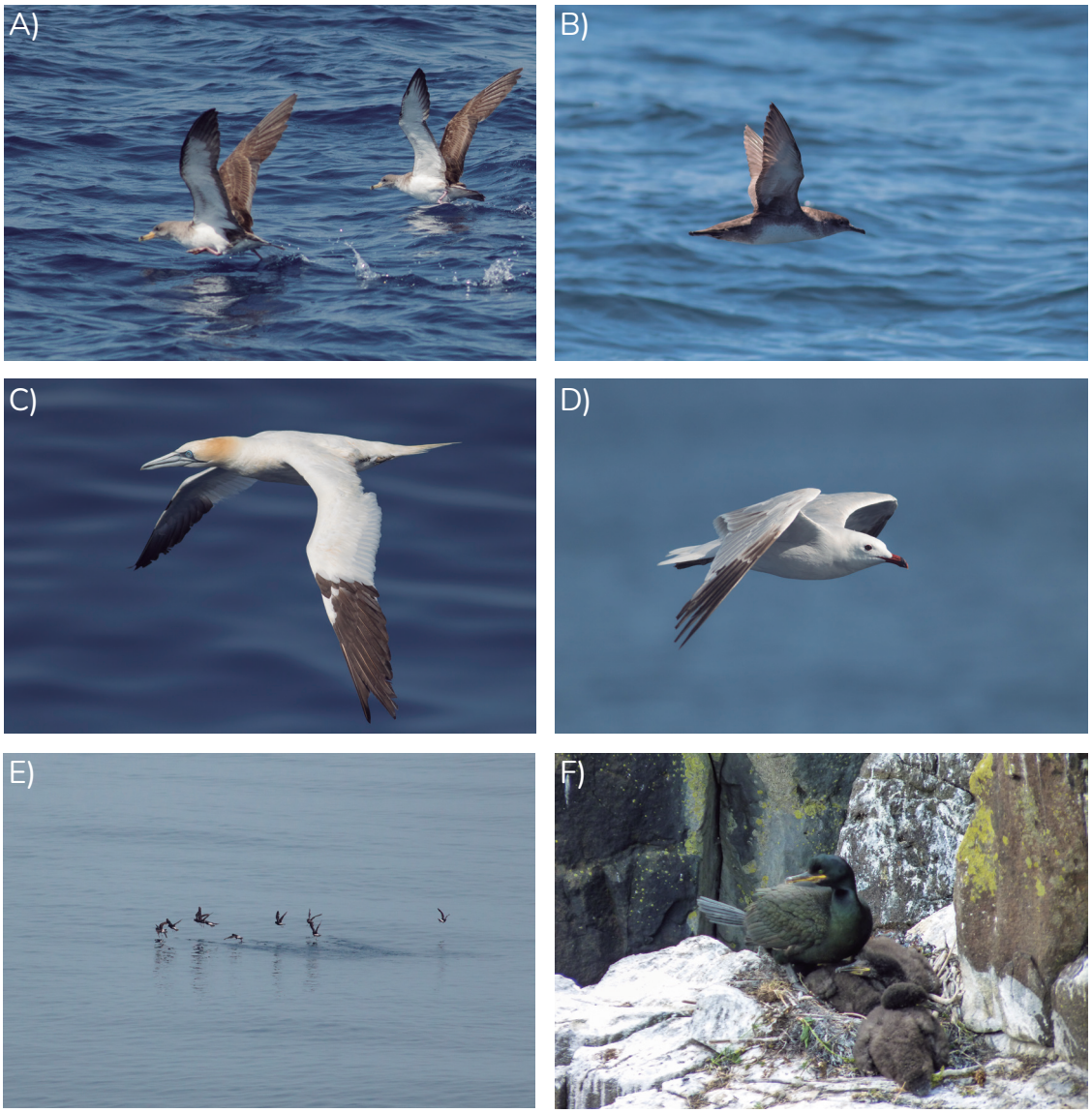


Imagen 2. Especies de aves marinas estudiadas en los diferentes trabajos que componen esta tesis doctoral. A) Pardela cenicienta atlántica *Calonectris borealis* (izquierda) y pardela cenicienta mediterránea *Calonectris diomedea* (derecha). B) Pardela balear *Puffinus mauretanicus. C)* Alcatraz atlántico *Morus bassanus.* D) Gaviota de Audouin *Ichthyaetus audouinii.* E) Paíño común o europeo *Hydrobates pelagicus.* F) Cormorán moñudo *Gulosus aristotelis.*

Censos desde barco y revisión bibliográfica

El registro de datos referente a la avifauna del Golfo de Cádiz se realizó mediante las prospecciones anuales de las campañas ECOCADIZ del Instituto Español de Oceanografía (IEO) a bordo de los buques oceanográficos 'Cornide de Saavedra' (2006-2013) y 'Miguel Oliver' (2014-2019). Estas campañas tienen como objetivo principal la evaluación acústica de las poblaciones de pequeños peces pelágicos sobre la plataforma continental del Golfo de Cádiz (profundidad <200 m) (Massé *et al*., 2018), si bien en los últimos años han ampliado sus objetivos desde un enfoque más ecosistémico, e incluyen, entre otros, el seguimiento mediante censos de depredadores apicales (aves marinas, tortugas y cetáceos).

Los censos desde barco se realizaron en verano (junio-agosto) y se contabilizaron las aves marinas siguiendo los protocolos estándares europeos de aves marinas en el mar mediante transectos predeterminados (Tasker *et al*., 1984; Camphuysen *et al*., 2004). Todas las observaciones se registraron durante buenas condiciones climáticas y se unificaron en unidades de prospección o secuencias de 10 minutos de duración a velocidad constante del barco (10 nudos) con el fin de estandarizar los esfuerzos en diferentes años.

Para la investigación llevada a cabo en el archipiélago de las Islas Berlengas, se realizó una búsqueda bibliográfica de toda la información dispersa sobre la biología y ecología del cormorán moñudo relevante para el estudio. Del mismo modo, se identificaron todas las posibles causas de declive poblacional a la vez que se cuantificaron todas aquellas presiones, impactos y molestias que fueran de interés en el estudio demográfico de la especie. Para obtener esta información se utilizaron los principales buscadores de literatura científica, revisándose más de 100 documentos entre artículos científicos, secciones y capítulos de libros, monografías sobre la especie, atlas y anuarios ornitológicos, presentaciones y actas de congresos, informes y reportes administrativos, páginas web y comunicaciones personales. Esta revisión se realizó sobre documentos tanto en inglés, portugués como español.

Imagen 1. Instantánea tomada durante censo de aves marinas en una de las campañas ECOCADIZ del Instituto Español de Oceanografía (IEO) a bordo del buque oceanográfico Miguel Oliver. © Eli Muñoz.

Modelado de hábitat y poblaciones

A lo largo del desarrollo de los trabajos que componen esta tesis doctoral, se han aplicado diversas técnicas de modelado a diferentes aspectos ecológicos de las especies marinas estudiadas para tratar de dar respuesta a los objetivos y preguntas específicas que se planteaban en cada capítulo. En particular, en los diferentes trabajos se han desarrollado modelos de distribución espacial (MDE) de especies, junto a modelos demográficos dinámicos. Ambos se utilizan cada vez más para comprender y predecir el futuro de las poblaciones de aves frente a potenciales amenazas (Bastos *et al*., 2016; Jenouvrier *et al*., 2018; Reisinger *et al*., 2018). Las herramientas de modelado han mejorado el conocimiento sobre la distribución y las tendencias poblacionales de especies y, en consecuencia, la identificación de áreas prioritarias y las medidas de gestión apropiadas para asegurar la conservación de las especies (Louzao *et al*., 2009; Arcos *et al*., 2012; Bastos *et al*., 2012).

Modelos de distribución espacial

Por un lado, el conocimiento y modelado de la distribución espacial de las especies de aves marinas y sus presas en el ámbito de estudio han sido pieza fundamental en el desarrollo de estas investigaciones. Los MDE para organismos altamente móviles, como son las especies de aves marinas, se basan en los registros de su ocurrencia y la relación con otras especies –p. ej. otras aves marinas o las presas sobre las que se alimentan– o con la variabilidad oceanográfica del medio donde habitan (Franklin, 2010). Llegar a comprender los mecanismos que determinan la distribución de las aves marinas resulta particularmente difícil (Fauchald, 2009), sobre todo porque el dinamismo de corrientes oceánicas, los vientos predominantes, movimientos de mareas, diferentes gradientes de salinidad, afloramientos y aportes de nutrientes en lugares concretos, hacen que el mar sea un lugar tremendamente dinámico donde los procesos oceanográficos son tan complejos y están tan interrelacionados entre sí, que en muchas ocasiones, diferentes escalas espacio-temporales pueden enmascarar las relaciones de dichos procesos (Le Fèvre, 1987a; Renault *et al*., 2016).

A su vez, el registro de la avifauna marina simultáneamente a la evaluación del stock pesquero durante campañas oceanográficas abre la puerta a obtener relaciones directas entre depredadores-presa en eslabones más próximos en la cadena trófica.

Seguidamente, la aplicación de nuestros resultados en la creación de cartografía visual mediante sistemas de información geográfica ha resultado fundamental a la hora de poder presentar nuestros resultados de una manera clara y precisa. De esta manera, los resultados obtenidos plasmados en un mapa pueden ser utilizados por gestores y conservadores del medio, sin necesidad de conocer los pormenores de los análisis y cálculos realizados.

Modelos demográficos dinámicos

Por otro lado, para evaluar y predecir el desarrollo de las poblaciones de especies amenazadas, el análisis de viabilidad de sus poblaciones y la propuesta de medidas de gestión apropiadas son herramientas ampliamente utilizadas en la conservación de especies marinas (Velando & Freire, 2002; Oro *et al*., 2018). Estos modelos se basan en el conocimiento de los parámetros demográficos realistas de la especie a estudiar junto al diagnóstico preciso de las presiones –naturales y antropogénicas– que actúan sobre la población (Lande *et al*., 2003). La integración de estos factores en modelos de sistemas dinámicos proporciona la información necesaria para prever las tendencias de las poblaciones aplicando diferentes acciones de manejo hipotéticas. Este tipo de modelos permite además la incorporación de opiniones de expertos como variables en el modelo, además de predecir las consecuencias futuras de escenarios alternativos de manejo (Bastos *et al*., 2012; Weller *et al*., 2016).

Chapter I

How adequately are the critically endangered Balearic shearwaters protected by the Special Protection Areas (SPAs) for seabirds? A case study in the Gulf of Cadiz

Arroyo, G.M., **De la Cruz, A.**, Delgado, D., (2020). Global Ecology and Conservation 21, e00861. doi.org/10.1016/j.gecco.2019.e00861

ABSTRACT

The expansion of marine protected areas in pelagic areas has been crucial to achieve sufficient protection of the oceans. However, there is still some controversy about whether these protected areas actually cover the vital areas for some species. We investigate the summer distribution of the critically endangered Balearic shearwater and its overlap with the Special Protection Area for seabirds (SPA), using the Gulf of Cadiz as a case study. This area holds the SPA named Marine Area of Gulf of Cádiz, covering 2314.2 km^2. A dataset of nine years of vessel-based surveys between 2006 and 2017 was analyzed, using Kernel Density Estimation to generate the core area polygons for each year. The area located off the Bay of Cádiz, southeast of the mouth of the Guadalquivir, has revealed as a very consistent key area for this species during summer. This area, covering 1082 km^2, regularly hosted populations that exceeded the threshold for area of international importance (IBA criteria) for the species. The current SPA covers less than 40% of this new key area. The limitation in the number of years of monitoring and seasonal differences in the dataset used to establish the boundaries of the current protected area may be at the base of these discrepancies. This study emphasizes the importance of synthesizing and collecting long-term information to define marine protected areas and to assess their efficiency over the time. Furthermore, our study highlights the urgent need to expand this marine protected area to protect effectively this critically threatened species.

INTRODUCTION

In recent years marine protected areas (MPAs) have experienced considerable expansion (Boonzaier & Pauly, 2016; Hilborn, 2016), covering 7.3% (over 26 million km^2) of the world's oceans and 16.8% of coastal and marine areas under national jurisdiction by 2018 (UNEP-WCMC *et al*, 2018), thus advancing towards the goal of protecting 10% of the world's seas and oceans by 2020 (Convention on Biological Diversity, 2010). Nevertheless, debate still exists on the effectiveness of MPAs in achieving ecological and societal conservation targets (Claudet, 2018; Pendleton *et al*., 2018). To truly fulfil its goal for protecting biodiversity, the delimitation of MPAs must encompass the concentration areas of targeted organisms throughout the annual cycle, otherwise their effectiveness would be seriously compromised. However, the adequacy of the design of MPAs once declared has been poorly

tested (Rodrigues *et al*., 2004; Abecasis *et al*., 2014; Pérez-Jorge *et al*., 2015). In this sense, the quality of the baseline ecological information is an essential issue to be considered for identifying, designating and managing MPAs appropriately (Abecasis *et al*., 2014; Fulton *et al*., 2015). Furthermore, once they have been declared, the evaluation of their effectiveness and the level of objectives achievement are essential parts for an adaptive management strategy conservation of MPAs (Ronconi *et al*., 2012). In this sense, considering the temporal scale can facilitate a more efficient and dynamic management of the MPAs, allowing implementing rapidly adaptive management strategies in space and time in response to the shifting nature of the ocean (Maxwell *et al*., 2015). However, the majority of the studies that have led to the definition of MPAs suffer from limitations in time and resources for obtaining basic information. Moreover, in many cases, the monitoring programs of the MPAs are not carried out or do not include indicators and data that allow evaluating the achievement of the proposed objectives (Pendleton *et al*., 2018).

Marine predators are suitable biological indicators to identify and prioritize areas for marine conservation. On the one hand, they are generally long-lived, wide-ranging organisms that forage at high trophic levels, integrating long-term and large-scale processes and changes in marine ecosystems (Paleczny *et al*., 2015; Piatt & Sydeman, 2007). On the other hand, their distribution often overlaps with areas of important anthropogenic activities such as commercial fisheries, with which they often share the same prey, resulting in interactions related to food availability or bycatch (Pichegru *et al*., 2009; Breen *et al*., 2016).

The distribution of most of the marine pelagic predators is generally connected to a range of dynamic oceanographic processes that determine oceanic productivity and, correspondingly, prey availability (Hunt & Schneider, 1987). These processes interact at different temporal and spatial scales, being generally difficult to establish what variables are relevant to determine this distribution without adequately considering both intra and inter annual variability at different spatial scales (Hyrenbach *et al*., 2000). Nevertheless, the occurrence of persistent oceanographic phenomena at regional scale as oceanographic fronts give rise to suitable foraging habitats that attract a large number of marine predators, and therefore constitute potential priority areas for conservation of multiple marine vertebrate taxa (Scales *et al*., 2014). In this sense, the consistency and spatiotemporal predictability of these foraging habitats are key aspects to assess their ecological importance (Augé *et al*., 2014; Scales *et al*., 2014; Meier *et al*., 2015) and consequently enhance the relevance of the core areas for preservation (Ramírez *et al*., 2016).

The implementation of the 1979 Birds Directive (2009/147/EC) in the European Union marine waters has led to the by designation of the Special Protection Areas (SPAs) for seabirds, in the framework of the Natura 2000 Network. In this regard, the Important Bird and Biodiversity Areas (IBA) Programme of BirdLife International has been recognized by the EU as a reference in the identification and designation of the SPAs (ICES, 2006; Ramírez *et al*., 2017). The pioneering works of SEO/BirdLife to identify marine IBAs in Spanish marine waters (Arcos *et al*., 2009, 2012), along with a sister project in Portugal (Ramírez *et al*., 2008), not only provided the first complete and comprehensive marine IBA inventories worldwide, but also settled the methodological framework to guide the identification of IBAs for seabirds in open sea waters. Since then, more than 1200 marine SPAs have been declared in 23 countries of the UE, representing 3,9% of the total EU marine area (Ramírez *et al*., 2017). However, significant deficiencies have been identified in the implementation process, such as the inherent lack of research resources and data in many European coastal states. Even in those countries that have led the process, deficiencies have been recognised in the availability and quality of the dataset used (Arcos *et al*., 2009, 2012; Critchley *et al*., 2018). In many of the studies that led to the definition of these protected areas the data were collected only for a limited time span within seasons, across seasons, and for a very limited number of years. These deficiencies may lead to the resulting protected areas suffering from inappropriate boundaries, which do not adequately cover the key areas throughout the annual cycle, nor adequately reflect inter-annual variability (Adams *et al*., 2012; Dias *et al*., 2017; Critchley *et al*., 2018).

In this study, the spatial distribution of the Balearic shearwater *Puffinus mauretanicus* (BSH hereafter), the most threatened seabird in Europe and listed as critically endangered (BirdLife International, 2018b), is analysed at regional level in the Gulf of Cadiz during early summer. The research analyses data of nine years of vessel-based surveys in the period 2006-2017, by means of spatially-explicit models of bird density using Kernel Density Estimation (KDE) (O'Brien *et al*., 2012), to identifying potential hotspots of high bird abundance across years. Thus, the consistency in the distribution areas was evaluated by measuring the inter-annual variability of the KDE. Furthermore, annual bird abundances into the core area were estimated in order to assess the population occurring within the areas of aggregation against the 1% IBA criteria (Skov *et al*., 2007). Finally, spatial overlap of the current SPA Gulf of Cádiz (ES0000500) with the at-sea distribution of this species during summer was examined.

METHODS

Study Area

The study area covers most part of the Gulf of Cádiz. It includes the marine area off the Algarve region, in the southern coast of Portugal and the Atlantic side of Andalusia Region, off the southwest coast of Spain (36°00' to 37°00' N and 5°45' to 9°00' W). The area extends from Cape Trafalgar in the Spanish coast to Cape St. Vincent in Portugal over 390 kilometres of coastline and a total area of ca. 17500 km^2 (Fig. 1a).

At-sea survey data

Vessel surveys were conducted over nine years between 2006 and 2017, during early summer (June to early August; see Table A.1). This period corresponds to post-breeding migration of BSH, when the majority of its population leaves the Mediterranean passing through the Strait of Gibraltar (Arroyo *et al*., 2016) spending considerable time in the Gulf of Cadiz (Pérez-Roda *et al*., 2017).

During surveys, seabirds were counted at one or two sides ahead of the vessel depending on census conditions, following standard European Seabirds at Sea protocols for data collection (Tasker *et al*., 1984; Camphuysen *et al*., 2004). All the observations were collected during good weather conditions (wind force under 6 Beaufort scale; visibility range ≥ 1000 m; no rain; Webb & Durinck, 1992) and summed up into 10 min survey sequences (survey units) during constant speed of the vessel (10 NM) in order to standardize the results over the years.

Spatial pattern analysis

Presence data were used to identify important concentration areas of BSH in summer based on KDE (O'Brien *et al*., 2012). ArcGis 10.5 Kernel Density Tool (ESRI, 2016) was used to generate the core area polygons (CA hereafter; Fieberg & Kochanny, 2005), here defined as the area accounting for 50% of the bird locations collected for the species during each year (50% utilization distribution contour). For some years, CA results produced more than one polygon. In these cases, those polygons whose size supposed less than 10% of the total CA were removed, otherwise multiple polygons were kept.

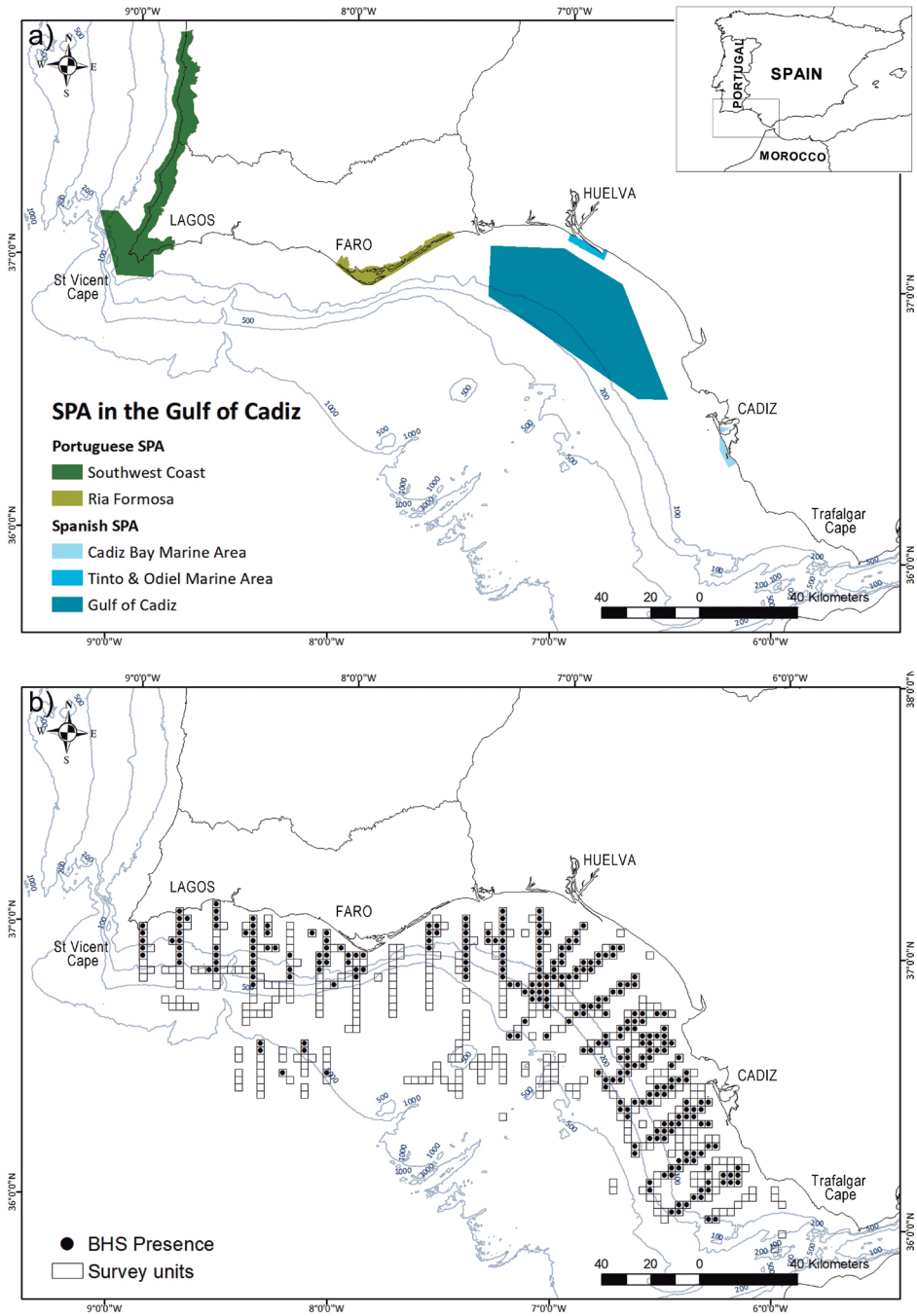


Figure 1. Maps of the study area with geographic references a) location of the Marine SPA - Nature 2000 Network in the area of study, the Gulf of Cadiz; b) Representation of the sampling effort in the study area (black points represent survey units with presence of BSH; empty squares represent absences).

Inter-annual spatial consistency and overlap with conservation areas

Inter-annual consistency in CA location was evaluated by measuring the overlap of CA polygons among years, following the methodology described in Meier *et al*. (2015). The Volume of Intersection Index (VI) (Seidel, 1992) was calculated as a statistical measure of overlap between CA for each pair of years, implementing the R functions from Fieberg (2014) (R Development Core Team, 2019). The values of VI range from zero (no overlap) to 1 (identical utilization distributions) (Fieberg & Kochanny, 2005).

Density analyses

Estimates of BSH numbers were assessed for each year in the CA. For this purpose, birds detected in the first 300 m band were used to estimate the relative density. The range of distances was measured using a hand-range finder (Heinemann, 1981). Density values per year were averaged from all survey units within the CA and these estimates were projected to the whole CA surfaces to obtain annual estimates of the total the population occurring within the CA, provided that these counts were representative in number and coverage (Arcos *et al*., 2012). Bootstrap resampling (1000 iterations) was used to assess 95% confidence intervals (Quinn & Keough, 2012). These yearly figures were compared with the most recent global population estimates (Arroyo *et al*., 2016) to assess the population occurring within the areas of aggregation against the 1% IBA criteria (Heath & Evans, 2000; Skov *et al*., 2007).

It was assumed that all birds inside the 300 m band were detected. It was not possible to correct density estimates for detectability since required parameters (particularly, the exact perpendicular distance of birds from the transect line) were not systematically recorded throughout the study period. Bird detectability may decrease significantly with the distance to the observer, leading to underestimates of actual seabird densities. Thus, figures resulting from this study should be regarded as conservative, providing a minimum number of birds per unit area.

RESULTS

Seabird distribution and consistency

Ninety-three vessel-based surveying days were conducted in early summer in the Gulf of Cadiz, totalling 294.3 hours of observation and 1766 survey units, throughout all the years (Table A.1). A total of 3053 BSH were observed in 389 survey units (22.0%). The average number of individuals per kilometre of survey effort was 0.56 (±3.55). In the 19.3% of survey units only 1 to 10 birds were counted, whereas congregations of more than 50 BSH were observed in only 13 units throughout the study period (0.74 % of survey units).

The KDE analysis produced 16 polygons for BSH, based on 50% utilization distribution contour (Table A.2). Two polygons accounting for less than 10% of the annual surface were finally rejected for producing the CA (see shaded lines in Table A.2). The yearly surface included within the CA averaged was 1731.1 (±355.3) km^2.

The location of CA differed slightly among years (Fig. 2). The zone located southeast of the mouth of the Guadalquivir River in front of the Bay of Cádiz (between the meridians 36° 50'N-36°20'N) was part of the CA in 7 out of the 9 years analysed. The second concentration zone extended from the mouth of the Guadalquivir towards the northwest off to Doñana National park coasts and the mouths of the rivers Tinto and Odiel, reaching the area off the Guadiana River mouth in some years (longitude 6° 59'W). Both areas were used simultaneously in several years (2007, 2009, 2010 and 2017). In 2009, a small polygon off the Ria Formosa lagoon in the Algarve accounted for the 10% of the BSH, whereas in 2016 the birds displaced to the south-east, reaching the zone off Cape Trafalgar.

CAs showed a notably high overlap among years (VI =0.39±0.18; range=0.00–0.68; Table 1). In a third of the two-year combinations the VI value was higher than 0.50, whereas this value was close or equal to zero only in 2 out of 36 combinations (2010-2016 and 2015-2016).

When locations were pooled over the nine years surveyed, the resulting CA contour revealed that the key area for BSH in early summer in the Gulf of Cadiz extends towards southeast of the mouth of the Guadalquivir River, off the Bay of Cadiz, covering a surface of 1082 km^2 (Fig. 3). The current SPA only encompasses a small part of this key area (37.4%).

Annual abundance estimates.

Estimates of BSH numbers in the CAs markedly varied among years (Table 2). BSH abundance averaged 6680 birds (±4063) considering the 9-years data. The lowest value of BSH abundance was observed in 2016 with 700 birds (CI95%: 288 – 1319), whereas the highest value was observed in 2009 with 13 262 birds (CI95%: 4694 – 22241). The 1% threshold needed to reach the IBA criterion for BSH (250 birds; Arroyo *et al*., 2016) was widely exceeded in all 9 years.

Table 1. Pairwise overlap (%) of core areas (50% utilization distribution contours) for BSH between pair of years, compared with the volume of intersection (VI) Index (Seidel, 1992).

	2007	**2009**	**2010**	**2013**	**2014**	**2015**	**2016**	**2017**
2006	0.60	0.53	0.60	0.46	0.62	0.49	0.08	0.43
2007		0.38	0.68	0.31	0.55	0.64	0.04	0.45
2009			0.38	0.48	0.55	0.27	0.19	0.41
2010				0.32	0.43	0.57	0.01	0.40
2013					0.56	0.17	0.18	0.26
2014						0.36	0.19	0.31
2015							0	0.54
2016								0.54

Table 2. Annual abundance estimates of the BSH in the respective CA and the worldwide IBA criteria threshold for the species (250 individuals; Arroyo *et al*. 2016).

Year	**CA Surface (km^2)**	**Average Density (no. of birds/km^2)**	**Estimated Abundance (no. of birds)**	**+95%CI**	**-95%CI**
2006	1956.9	5.82	11397	4982	25638
2007	2024.7	3.39	6864	2796	19267
2009	2073.4	6.40	13262	4694	22241
2010	1165.1	3.59	4179	1798	12519
2013	1309.4	5.38	7046	943	32586
2014	1389.9	4.47	6212	2919	14970
2015	1803.4	1.15	2077	1104	3841
2016	2098.6	0.33	700	288	1319
2017	1758.7	4.76	8377	6038	12701

DISCUSSION

The declaration of marine SPAs has undoubtedly been a milestone in the conservation of the marine environment in EU marine territorial waters (Ramírez *et al*., 2017). The process for its definition and delimitation has been undertaken in a highly rigorous way, using different complementary approaches that allow obtaining quite consistent protected areas (Arcos *et al*., 2012; Louzao *et al*., 2012). However, recent works have revealed that these protected areas may have certain deficiencies to cover the distribution ranges of key the species throughout the annual cycle and that some key areas may have been left outside the boundaries of the protected areas (Dias *et al*., 2017; Critchley *et al*., 2018). The assessment of the effectiveness by means of consistent monitoring programs allows to improve the conservation value of MPAs and, eventually, to refine the MPA boundaries (Ronconi *et al*., 2012).

Are the key areas for Balearic shearwaters in summer properly protected by the SPA?

The present study demonstrates that the key areas for Balearic shearwaters in the Gulf of Cadiz are under-represented by current protected areas for pelagic seabirds. The area located off the Bay of Cádiz southeast of the mouth of the Guadalquivir has revealed as the key area for this species in summer in most of the years. This area is displaced southeast of the current SPA, and less than half of its surface is covered by the current protected area. While the results of our study are circumscribed to a regional (meso-) scale, they reveal a much more widespread problem about the adequacy in the design of pelagic MPAs for highly mobile pelagic marine species (Game *et al*., 2009).

For seabird species breeding in Britain and Ireland, Critchley *et al*., (2018) found a low overlap of MPAs with projected distributions of seabird populations, particularly for pelagic foraging seabirds, which are in general more threatened than coastal species (Croxall *et al*., 2012). At a wider scale, in the South Atlantic Ocean, Dias *et al*., (2017) found no overlap between the areas used most intensively by six pelagic species of seabirds and any of the existing MPAs in the South Atlantic Ocean. This is not an problem exclusive to seabird species, since in relevant marine regions for biodiversity, such as the Mediterranean Sea, there is a very low (<2%) overlap between existing marine protected areas and the main areas of conservation concern for biodiversity, including different groups of marine organisms (Coll *et*

al., 2012). Other studies, however, have revealed a relatively high coverage of the boundaries of Natura 2000 sites regarding the distribution of seabirds (Garthe *et al*., 2012),particularly in the case of BSH in Spain and Portugal (Meier *et al*., 2015; Araújo *et al*., 2017; Pérez-Roda *et al*., 2017). In this sense, whereas the general patterns of the design of MPAs at national level may be adequate, some site- and season- specific deficiencies can affect the global effectiveness of the MPA network. Therefore, specific monitoring programs at each site level are essential to ensure the proper functioning of these protected areas.

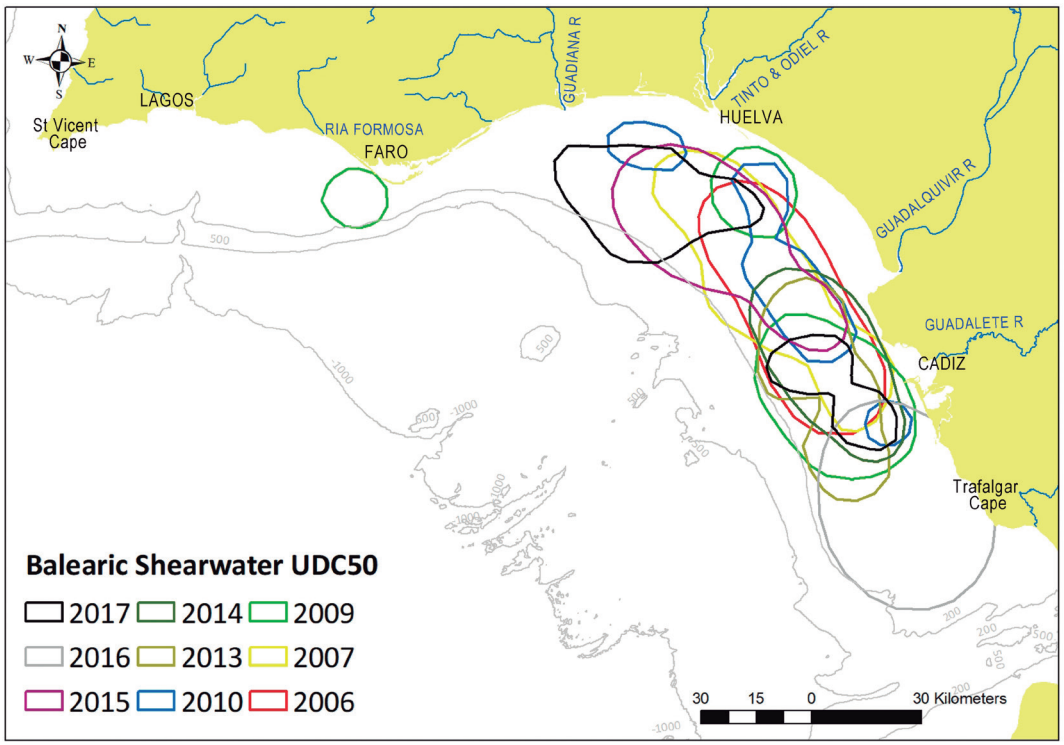


Figure 2. Locations of the core area (50% utilization distribution contour) polygons of Balearic shearwater over the years in the Gulf of Cadiz.

Are the key areas for the species consistent over time?

This study compiles information from nine surveying years, thus allowing analysing the consistency among years, which is important for understanding the stability of key sites over time (Tancell *et al*., 2013; Robertson *et al*., 2014; Meier *et al*., 2015). Foraging areas of seabirds may shift from year to year (i.e. Robertson *et al*., (2014b); Warwick-Evans *et al*., (2016), and short term surveys with limited inter-annual replication may fail to account for this variability.

Our study revealed that the CAs of the BSH in the Gulf of Cadiz were used repeatedly from year to year, with values of inter-annual overlapping higher than previously registered for this species during breeding period (Meier *et al*., 2015). Consistency of temporal and spatial pattern favour the definition of actual core areas for conservation (Ramírez *et al*., 2016). Site consistency for seabirds is typically attributed to the occurrence of persistent oceanographic features that favour the use of foraging seabirds (Hyrenbach *et al*., 2000; Scales *et al*., 2014). BSH distribution has been related to shallow, productive shelf areas with elevated chlorophyll a concentration and spatial gradients reflecting highly productive areas, both during breeding (Louzao *et al*., 2006a) and non-breeding seasons (Pérez-Roda *et al*., 2017). High chlorophyll a concentration has been argued as the main explanatory factor of the occurrence of foraging individuals in other species of procellariforms (Moore & Abbott, 2002; Maite Louzao *et al*., 2012; Kazama *et al*., 2019), whereas the chlorophyll gradient reveals the occurrence of fronts and eddies which locally increase productivity and aggregate small pelagic fishes in a predictable manner (Bellido *et al*., 2008).

Recent research has demonstrated that BSH spending more time in the Gulf of Cadiz during non-breeding season were related to warmer areas with low water mass variability and chlorophyll values (Pérez-Roda *et al*., 2017). Whereas chlorophyll concentration may be a direct proxy of primary production, BSH are top predators whose main trophic source consists on small pelagic fish available naturally and demersal fish available from trawling discards (Arcos & Oro, 2002; Käkelä *et al*., 2010; Louzao *et al*., 2011a). In this sense, the seasonal and inter-annual changes in the availability of natural potential prey species at meso-scale are driven by complex interactions of several factors acting at different spatial and temporal levels (García Lafuente & Ruiz, 2007; Teodósio *et al*., 2017).

Assessment of population importance: the 1% IBA criteria

To qualify as an IBA, a given area requires holding regularly over 1% of the global, regional or sub-regional population of those species for which the site has been selected (Heath & Evans, 2000; Skov *et al*., 2007). The Gulf of Cadiz SPA was designated especially for the important concentrations of four seabird species, including BSH (Arcos *et al*., 2009). The global population of this species has been recently re-assessed to 24500-26000 birds (Arroyo *et al*., 2016). In this study, the figures show that the core areas of Gulf of Cadiz have regularly been receiving more than a third of the BSH individuals in summer. Even if it is assumed that these can be relatively inaccurate estimates, they provide a figure of total birds using the area 'simultaneously' (Arcos *et al*., 2012), and its persistence over the years corroborates this area as a site of global key importance to this critically endangered species during non-breeding season. Our results also agree with those of Pérez-Roda *et al*., (2017), who observed that the Gulf of Cádiz was the area most frequently visited out of the breeding range by GLS-tracked individuals of BSH.

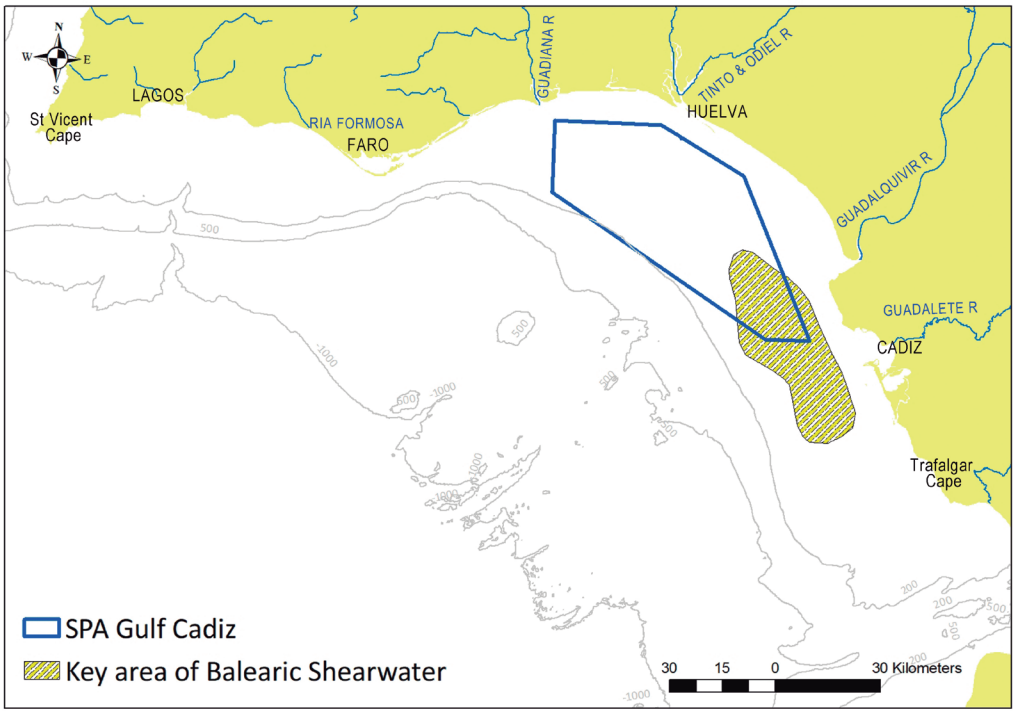


Figure 3. Key area of Balearic shearwater in the Gulf of Cádiz (considering all locations pooled over the nine years) and its overlap zone with the SPA Gulf of Cádiz.

Implications for Conservation: the need to expand the SPA Gulf of Cadiz.

The present study has revealed that the main key area for the critically endangered BSH during the summer season in the Gulf of Cadiz is not adequately protected by the current SPA. These results, however, do not invalidate the current limits established for the SPA (Arcos *et al*., 2009). In this sense, the discrepancies between the core areas described here and the current SPA can be explained by different causes. In the process that conducted to IBA's identification, Arcos *et al*., (2009) recognized the poor accuracy of the data, coming from only three years of campaigns. In this sense, this research also highlights the importance of synthesizing and collecting long-term information to define marine protected areas and other conservation schemes in a context of global change from an adaptive perspective. This requires the maintenance of long-term monitoring programs for the conservation of seabirds (Grémillet & Boulinier, 2009). These long-term data analyses allow the designation of SPAs that account for at least mid-term dynamic distribution patterns within protected sites (Garthe *et al*., 2012).

On the other hand, when marine IBAs where proposed in Spain, several representative pelagic species were used for seabird hotspots delimitation (Arcos *et al*., 2012). Despite single species (generally considered as 'umbrella' species) have been used in the identification of site-specific candidate MPAs (i.e. Oppel *et al*., 2012), a multi-species approach provides generally a better tool for effectively protecting marine species and ecosystems (Ronconi *et al*., 2012; Abecasis *et al*., 2014; Young *et al*., 2015). Thus, the current protected area provides protection to other species for which it was designated.

Moreover, the delimitation of the SPA in the Gulf of Cadiz was based on dataset collected in spring and autumn (Arcos pers.com.), both reflecting the relevance of the population of BSH in the current protected area during those periods. The Gulf of Cadiz is characterized by its strong seasonality (García Lafuente & Ruiz, 2007; Prieto *et al*., 2009; Caballero *et al*., 2014). The interaction between changes in oceanographic conditions, food resources and the phenology of the species leads to variations in species distributions throughout the year at different spatial levels, and this is an essential issue to be considered when designating MPA networks regarding highly mobile marine predators (C. Lambert *et al*., 2017c).

Recent studies have revealed strong seasonality in the patterns at sea distribution of cetaceans and seabirds in nearby areas (C. Lambert *et al*., 2017a; Pettex *et al*., 2017) which

can lead to variations in the relevance of hotspots for the conservation of these species throughout the year (C. Lambert *et al*., 2017b; Pérez-Roda *et al*., 2017). In this sense, the summer season corresponds to the post-breeding migration of BSH, when almost all Balearic shearwaters leave the Mediterranean through the Strait of Gibraltar (Arroyo *et al*., 2016), and are distributed in different feeding areas, the Gulf of Cádiz being one of the most frequently visited at that time (Pérez-Roda *et al*., 2017). Therefore, it is crucial to correctly protect the concentration area of this critically threatened species during this key period of its annual cycle. In this sense, our study highlights the urgent need to expand this marine protected area and provides the appropriate limits to carry out this extension.

Chapter II

Drivers for spatial modelling of a critically endangered seabird on a dynamic ocean area: Balearic shearwaters are non-vegetarian

De la Cruz, A., Ramos, F., Navarro, G., Cózar, A., Bécares, J. y Arroyo, G.M. (2021). Aquatic Conservation: Marine and Freshwater Ecosystem. doi 10.1002/aqc.3542

ABSTRACT

1. Spatial modelling is an important research tool to improve knowledge about the distribution of wildlife in the ocean. Using different modelling techniques (MaxEnt and Generalized Linear Mixed Model), a predictive habitat suitability model was developed for one of the most threatened seabirds in the world, the Balearic shearwater *Puffinus mauretanicus*.
2. Models were developed using a 10-year data set from the Gulf of Cadiz (south-western Iberian Peninsula), a key foraging area for Balearic shearwaters during migration and the non-breeding season.
3. Predictive habitat maps strongly matched the observed distribution patterns pointing at bathymetric features as main modelling drivers. The species concentrated on the shallow areas (up to approximately 100 m depth) of the continental shelf, particularly near the mouth of the River Guadalquivir. In contrast with previous studies, Balearic shearwater distribution in the highly dynamic Gulf of Cadiz was not correlated to areas of high chlorophyll-a concentration.
4. This lack of spatial correlation is probably due to the delay between the phytoplankton bloom and the response of the zooplankton and the small fish preyed upon by Balearic shearwaters, which may result in important displacements of this trophic chain across the Gulf of Cadiz.
5. The analysis presented contributes to a better understanding of the spatial distribution and ecology of the critically endangered top predator in the Gulf of Cadiz and offers important information to improve management plans.

INTRODUCTION

Species distribution models (SDMs) are increasingly used to understand and predict the pattern of biodiversity distribution, emerging as a key tool in ecology and biogeography research (Peterson *et al*., 2011; Reisinger *et al*., 2018; Fernandes *et al*., 2019). SDMs for mobile organisms are based on tracking or presence records of species and analyse the relationship between these records and the environmental characteristics at such sites (Franklin, 2010). Modelling tools have improved knowledge about species distribution and consequently the identification of conservation priority areas (Guisan & Thuiller, 2005; Sánchez-Carnero *et al*.,

2016). In the ocean, SDMs characterize habitats from an oceanographic point of view (Ballance *et al*., 2006), allowing the distribution of predators to be related to prey availability and oceanographic processes controlling productivity (Hunt & Schneider, 1987).

One of the most challenging aspects is to understand the mechanisms driving the distribution of marine organisms. In the highly oligotrophic open ocean, the appearance of patchy areas of high primary productivity, associated with oceanographic processes such as upwelling, oceanic fronts or eddies, create aggregation areas where relatively complex trophic webs develop, attracting a high number of top marine predators and resulting in biodiversity hot spots (Malakoff, 2004; Worm *et al*., 2005; Alves *et al*., 2018). The increasing development of satellite remote sensing techniques has revealed the relationships of marine predator distributions providing remote-sensed estimates of primary productivity (using chlorophyll-a concentration as a proxy) and Sea Surface Temperature (Polovina *et al*., 2004; O'Toole *et al*., 2017; Zainuddin *et al*., 2017). However, top marine predators do not feed on phytoplankton. Thus, in the intensely dynamic ocean with rapid and highly variable spatio-temporal changes (Maxwell *et al*., 2015), it would be expected that there is a decoupling between the processes controlling primary producers and the upper trophic levels of the food web (Le Fèvre, 1987; Renault *et al*., 2016). This phenomenon would result in a mismatch between primary productivity and the spatial ecology of marine top predators (Grémillet *et al*., 2008).

Effective management and conservation in the open ocean is highly dependent on understanding basic predator ecology (Game *et al*., 2009; Marshall *et al*., 2016; Guerra, 2019) and the processes driving their distribution (Afán *et al*., 2015; Gladics *et al*., 2015; García-Barón *et al*., 2019). The importance of this fact not only lies in the fact that top predators are key ecological indicators in marine ecosystems (Maxwell *et al*., 2013; Hazen *et al*., 2019), but also because many of them are facing severe conservation problems and are subject to protection measures regulated by law whose application is not always completely effective (Soulé *et al*., 2005; Lescroël *et al*., 2016).

Much of the planet's biodiversity is found in the ocean and yet the marine environment is clearly under threat and mostly unprotected (Jenkins & Van Houtan, 2016; Luypaert *et al*., 2019). In particular, seabirds are one of the most threatened groups within the marine environment and their populations have declined globally by almost 70% in the last century

(Paleczny *et al*., 2015; Dias *et al*., 2019). The establishment of Marine Protected Areas (MPAs) has become one of the most pragmatic approaches to mitigate the biodiversity loss (Hyrenbach *et al*., 2000; Davidson & Dulvy, 2017; Handley *et al*., 2020), and seabirds are effective proxies for identifying priority conservation sites for themselves and other taxa (Brooks *et al*., 2001). Among seabirds, the Balearic shearwater (*Puffinus mauretanicus*) is one of the most threatened species in the world (Oro *et al*., 2004; Genovart *et al*., 2016; Birdlife International, 2020). This species, endemic to the Balearic Islands, is listed as 'Critically Endangered' on the International Union for Conservation of Nature (IUCN) Red List (Birdlife International, 2020).

Balearic shearwaters are easily monitored and cross different and very dynamic areas during their migration, from their breeding areas in the Mediterranean Sea, transiting the Strait of Gibraltar and reaching the North Atlantic (Guilford *et al*., 2012). Moreover, they prey on different species of pelagic fish and other marine organisms (Käkelä *et al*., 2010). Therefore, its conservation status may reflect the conditions of the environment where they are found, acting as an indicator species (Siddig *et al*., 2016). Its population size is estimated at around 25,000 individuals (Arroyo *et al*., 2016) and demographic modelling shows a severe decline and predicts its extinction within a few decades (Genovart *et al*., 2016). Balearic shearwater leave the Mediterranean heading to the Atlantic ocean from mid-May to mid-July and return to the breeding grounds from late August, peaking in October (Guilford *et al*. 2012, Arroyo *et al*. 2016). The Gulf of Cadiz (GoC, Figure 1) is part of its flyway migratory corridor and plays an important role as a foraging area (Arcos *et al*., 2009). Therefore, GoC has been identified as a marine Important Bird and Biodiversity Area (IBA) (Arcos *et al*., 2009) and Special Protected Area (SPA) due to its relevance for the Balearic shearwater among other seabird species (BOE, 2014).

Species distribution models have been widely used to determine the most suitable habitat for the Balearic shearwater (Louzao *et al*., 2006a, 2012; Meier *et al*., 2015; Araújo *et al*., 2017), being decisive when identifying the marine IBA of GoC and with it the legally-binding SPA for protection of the species (Arcos *et al*., 2012; BOE, 2014). Based on a significant improvement in the monitoring of this species in the GoC, the aim of this study was to advance the understanding of the distribution of the Balearic shearwater, analysing the contemporary oceanographic features influencing the distribution of the species in the region. Considering previous knowledge, we hypothesize that dynamic variables related to

ocean productivity drive the occurrence of Balearic shearwater in the GoC. Consequently, a higher probability of occurrence of Balearic shearwater in those areas with higher primary production would be expected (Louzao *et al*., 2011b; Louzao *et al*., 2012; Araújo *et al*., 2017). Alternatively, in very dynamic marine areas, other oceanographic processes could mask the relationships between primary production and the presence of top predators (Croll *et al*., 2005).

METHODS

Study area

The distribution and essential habitat of the Balearic shearwater were studied in the GoC over 10 years between 2006 and 2018 during the postnuptial migration period (Table S1, supplementary material). The surveyed area covered from Cape St. Vincent in the Algarve (off the southern coast of Portugal), to the Atlantic coast of Andalusia (off the south-west coast of Spain) until Cape Trafalgar (i.e. 36°00' to 37°00' N and 5°45' to 9°00' W), encompassing 390 kilometres of coastline and a total area with almost 20,000 km^2. This area was studied during the annual summer ECOCADIZ acoustic-trawl surveys conducted by the Spanish Institute of Oceanography (IEO) on board the R/V 'Cornide de Saavedra' (until 2013) and subsequently the R/V 'Miguel Oliver' to acoustically evaluate the small pelagic fish populations over the GoC continental shelf (depth <200 m) (Massé *et al*., 2018).

This is an important area for seabirds with five SPAs designated under the 1979 Birds Directive (2009/147/EC) (European Commission, 2009) as part of the Natura 2000 network. On the Spanish side these are the Gulf of Cadiz (ES0000500), the Tinto and Odiel Rivers (ES0000501), and the Bay of Cadiz (ES0000502) (BOE, 2014), whilst on the Portuguese side there is the south-west coast (PTZPE0015) and Ria Formosa (PTZPE0017) (Figure 1).

The GoC region is characterized by strong seasonality and important synoptic meteorological events (Prieto *et al*., 2009) which largely control chlorophyll-a concentrations and suspended material (Caballero *et al*., 2014). In this basin, important river flow (Guadiana, Guadalquivir, Tinto-Odiel, etc.) fertilize the coastal fringe, reaching high chlorophyll-a concentrations throughout the year (Navarro & Ruiz, 2006). The shelf zone between Trafalgar and Santa Maria Capes embraces favourable features and sustain a high concentration of fish eggs, larvae (Baldó *et al*., 2006) and small pelagic fish (Ruiz *et al*., 2009).

At-sea data collection and processing

Vessel-based surveys were conducted in early summer (June to early August; Table S1, supplementary material). During surveys, seabirds were counted on one or both sides ahead of the vessel depending on census conditions following the standard European Seabirds At Sea (ESAS) protocols (Tasker *et al*., 1984; Camphuysen & Garthe, 2004). Snapshot counts were used to count flying birds (Tasker *et al*., 1984). All the observations were registered during good weather conditions and summed into 10 min survey units with the vessel travelling at a constant speed of 10 knots in order to standardize the measurements over several years. A binary value of '1' was assigned to each 10 min sequence in which the presence of the Balearic shearwater was recorded (hereafter referred to as 'presence') (Figure 1), whereas sequences where no Balearic shearwater were observed were coded as '0' (hereafter referred to as 'absence'). This presence/absence was considered as the dependent (response) variable. Data on abundance (i.e. density) was not considered in this research.

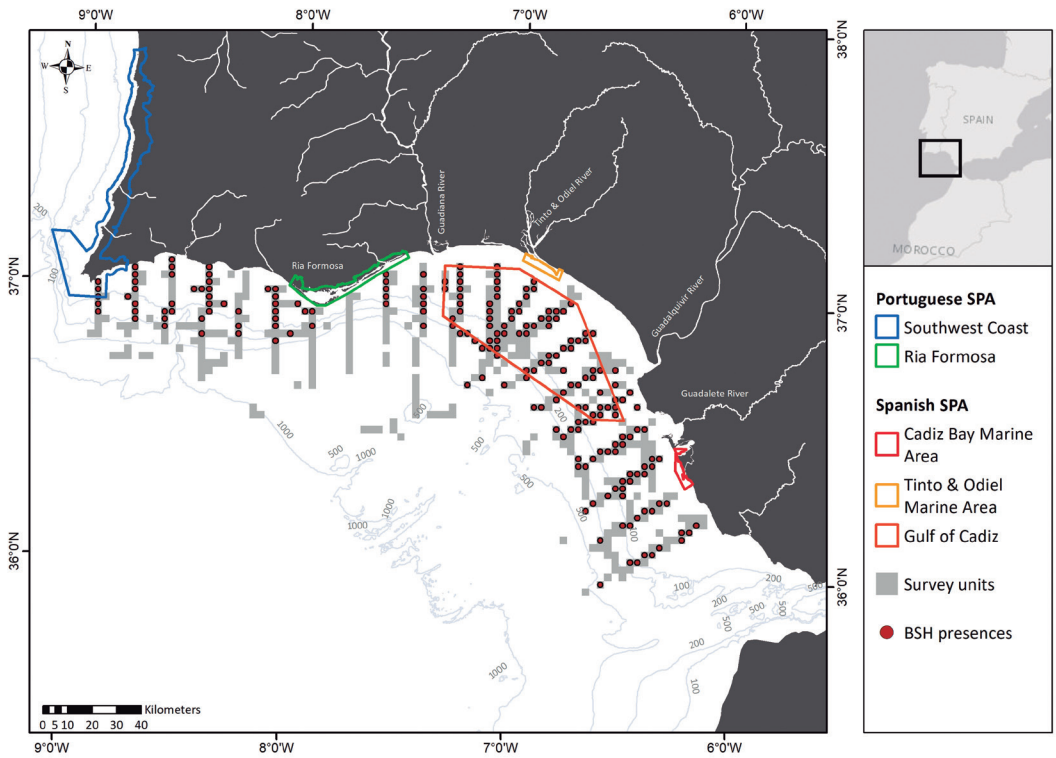


Figure 1. Overview of the study area with river references and Gulf of Cadiz Special Protection Areas. Red dots represents BSH presences in the 10 minutes surveys units (grey square). Coloured polygons represent the Special Protection Areas (SPA) in the Gulf of Cadiz. Main bathymetric profile and main rivers of the area are showed.

Environmental variables description and selection

A set of ecologically relevant predictors (static and dynamic) were selected to characterize the marine environment as proxies for physical and biological processes potentially driving the Balearic shearwater distribution in the GoC, based on previous knowledge on habitat selection of the species (Louzao *et al*., 2006b; Louzao *et al*., 2012; Araújo *et al*., 2017). The ecological basis for choosing variables are shown in Table S2 (supplementary material). Static (physical) variables (bathymetry, slope, distance to isobaths and distance to main coastal geographic features), were extracted and derived from EMODnet Bathymetry portal http://www.emodnet-bathymetry.eu (Marine Information Service, 2016). Dynamic oceanographic data, monthly chlorophyll-a concentration (CHL) and monthly sea surface temperature (SST), were extracted from Aqua MODIS satellite imagery via https://oceancolor.gsfc.nasa.gov/ at a spatial resolution of 4 x 4 km, and turbidity was derived using remote sensing reflectance from Aqua MODIS, following Caballero *et al*. (2014) (Table S2, supplementary material). When the survey took place over two months a new layer with the average of both months was calculated.

Colinearity between variables was investigated estimating pairwise Spearman-rank correlation coefficient by using R software (R Development Core Team, 2020). When a pair of environmental variables was highly correlated ($|rs|>0.65$), the most ecologically relevant one was chosen to be tested in the model (Table S3, supplementary material).

Distribution models performance

A comprehensive ecological modelling approach was followed to investigate the influence of environmental factors on the occurrence of Balearic shearwater by developing SDM. For this purpose, the performance of two modelling procedures was compared.

Annual distribution models

First, the effects of environmental variables on the presence of Balearic shearwater was investigated separately by year (annual distributions models), using the maximum entropy modelling technique, MaxEnt (Phillips, 2017; Elith *et al*., 2011). This approach has fewer information requirements, allows an estimation of the explanatory power of each environmental variable and is easily integrated with the graphical representations in the geo-

graphic information system (GIS), providing predictive distribution maps based on occurrence probability for each year, which has made it one of the most widely methods used to perform SDMs (Elith *et al*., 2006; Elith & Leathwick, 2009). Before running annual models, all data were prepared to be read by MaxEnt software. One of the requirements of MaxEnt is that all spatial information must be presented in the same format (i.e., wiith the same number and size of cells and the same geographic extension) for both the presence data for the species and for the environmental variables to be tested in the model. To obtain easily interpretable results, the predictive layers included in the model were restricted to the sampled area. Models were evaluated for each year using default datasets, randomly selecting a bootstrapping 25% as test data and removing duplicate values per cells to minimize autocorrelation biases and linear and quadratic relationships with a cloglog output for easier interpretation. In order to reduce the sample bias, a 'bias file' was used to represent the sampling effort each year. MaxEnt predictions were calculated 10 times in order to obtain an average prediction and coefficient of variation of predictions (Edrén *et al*., 2010). The Area Under the receiver operating characteristic Curve (AUC) was used to assess the predictive performance of each model (Fielding & Bell, 1997). The range of AUC values varies from 0 to 1 (from negligible to perfect discriminatory power, respectively). An AUC of 0.5 indicates that the performance of the model is equal to that of a random prediction, while values between 0.5 to 1 indicate the following performance classification: 1.0-0.9 excellent, 0.9–0.8 good, 0.8–0.7 reasonable, 0.7–0.6 poor and 0.6–0.5 unsuccessful (Engler *et al*., 2004).

Overall model

Data for the 10 years were pooled to investigate the overall effect of explanatory factors on the distribution of the species (overall model). In order to choose the best model to analyse presence-absence data (Brotons *et al*., 2004), Generalized Linear Mixed Models (GLMMs) with a binomial error distribution and logit link function were used (Zuur *et al*., 2009), with the help of the 'glmer' function from the 'lmer4' package using R (R Development Core Team, 2020). The factor year was settled as a random effect, and the variables retained after colinearity analysis (see above) were included as fixed factors in the GLMM model procedure. Logarithms of distance variables were calculated in order to avoid convergence problems and scale variable warnings. Model selection was made using the Akaike's information criteria (Akaike, 1973) to identify the most robust (i.e., including variables with the strongest im-

pact on outcomes) and parsimonious (i.e., avoiding over-fitting) models following a forward stepwise selection approach (Burnham & Anderson, 2002). When AIC values differences between models were low (ΔAIC less than 2), models with fewer variables were selected in order to maintain the most parsimonious model (Burnham & Anderson, 2002).

Spatial auto-correlation bias

Spatial auto-correlation (that is, locations close to each other show values that are more similar than those that are more distant) is a general statistical property of ecological variables observed across geographic space (Legendre, 1993; Dormann *et al*., 2007) that may be an important source of bias in most spatial analyses (Segurado *et al*., 2006). The occurrence of this spatial auto-correlation in residuals of distribution models means that the key assumptions of residuals being independent and identically distributed is violated, which can inflate the probabilities of falsely rejecting the null hypothesis (type I error) (Segurado *et al*., 2006; Dormann *et al*., 2007; Peres-Neto & Legendre, 2010). In these cases, spatial distribution models may overestimate the importance of environmental factors (Legendre, 1993; Dale & Fortin, 2002), generating an artificial matching between species distribution and modelling drivers (Legendre *et al*., 2002; Dormann *et al*., 2007). In this study the spatial auto-correlation of the residuals of the best models was assessed by calculating the Moran's auto-correlation Index (Moran, 1950), using the 'ape' library in the R software package (Paradis *et al*., 2004). Moran's I ranges from '-1' (perfect dispersion) to '+1' (perfect correlation), with values around zero indicative of a random spatial pattern. For each survey unit, the coordinates (latitude and longitude) of the initial unit were computed.

RESULTS

At-sea survey

One hundred and four vessel-based survey days were conducted in early summer in the GoC (Table S1, supplementary material), covering 2003 survey units and more than 333 hours of observation over the ten years of the study. Balearic shearwater were present in 420 units. Overall, most of the shearwaters were seen on the continental shelf off the coast of Cadiz Bay and near the mouth of the River Guadalquivir (Figure 1).

Annual distribution models

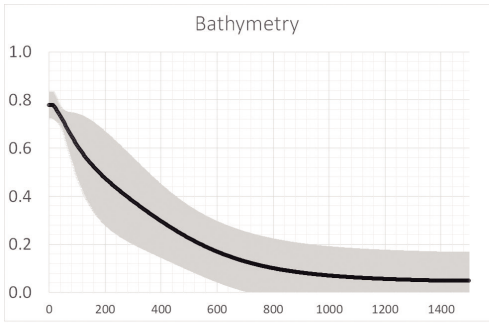
After colinearity analysis, the following parameters were retained to be tested against Balearic shearwater presence: 'Bathymetry', 'Distance to Guadiana river mouth', 'Distance to Guadalquivir river mouth', 'Distance to 200 m-Isobath', 'Chlorophyll-a concentration (CHL)', and 'Sea Surface Temperature (SST)' (Table S3, supplementary material).

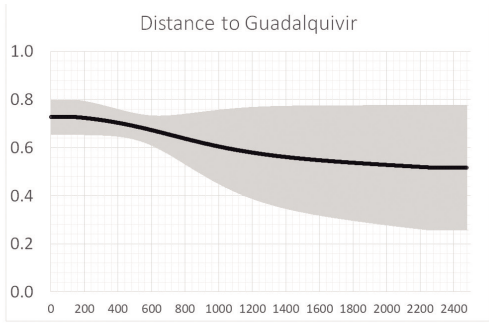
All annual distribution models for every single year of the study showed either a reasonable or good performance, with an average of 0.790 ± 0.06 (Table 1) and, in all cases static predictors contributed substantially more to model performance than dynamic ones. Moreover, the contribution of the different factors was quite consistent throughout the years of the study. Bathymetry was the most explanatory variable in the majority of the annual models (average contribution 36.60 ± 25.37%; Table 1). The probability of occurrence was maximum in shallow water, up to approximately 100 m and rapidly decreased beyond 200 m (Figure 2). The distance to the Guadalquivir river was the second factor most contributing to the performance of the models in the majority of the years (20.35 ± 16.56%; Table 1), with higher occurrence probability near its mouth (Figure 2). In some years (i.e. 2013 and 2015), the higher probabilities of occurrence moved to the west near the Portuguese waters, and then the 'Distance to Guadiana River mouth' or to the 'Distance to 200-m isobath' (shelf break) acquired more relative contribution (Figure 2; Table 1). These results show a remarkably consistent distribution of the Balearic shearwater in summer in the GoC, covering shallow waters near the coast between the mouths of the Guadiana and Guadalquivir rivers and extending towards the Bay of Cádiz, as reflected by most of the annual models (Figure 3).

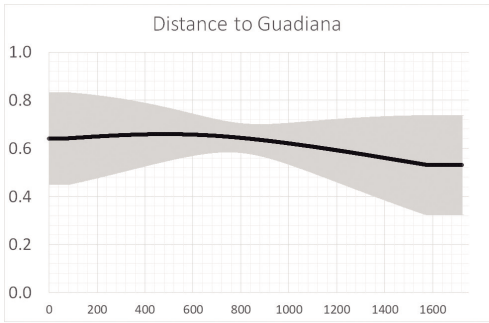
Table 1. Maxent analysis with the average results of 10 replicates. Mean Test AUC, its standard deviations (SD) and heuristic estimate of environmental parameters analysed models (bathymetry, distance to Guadalquivir river mouth, distance to Guadiana river mouth, distance to 200 m isobath, chlorophyll-a concentration and sea surface temperature), relative contribution (%) in each year and overall surveys are shown. First predictors with major contribution are showed in bold and second predictor in italic.

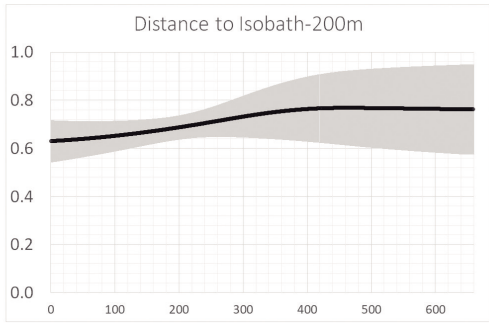
Survey	Test AUC	SD	Bathymetry	Dist Guadalquivir	Dist Guadiana	Dist 200 m Isobath	CHL	SST
2006	0.85	0.04	**60.87**	*16.93*	3.94	13	2.53	2.73
2007	0.75	0.06	**56.17**	*13.72*	7.55	12.85	9.63	0.08
2009	0.80	0.05	**46.66**	*18.94*	4.12	12.68	11.67	5.94
2010	0.89	0.03	*17.82*	15.37	9.59	**35.91**	17.79	3.53
2013	0.72	0.05	2.09	*17.97*	**50.14**	10.13	14.43	5.23
2014	0.77	0.04	15.1	18.4	*22.6*	**33.62**	10.17	0.11
2015	0.76	0.06	*35.49*	5.52	**45.63**	3.62	3.44	6.29
2016	0.73	0.07	**83.34**	1.39	*10.29*	3.53	1.3	0.14
2017	0.78	0.03	*34.8*	**35.22**	13.53	4.75	3.93	7.78
2018	0.84	0.05	*13.7*	**60.06**	13.06	10.05	2.99	0.15
Averaged annual	0.79	0.05	**36.6**	*20.35*	18.05	14.01	7.79	3.2
SD Averaged annual	0.06		25.37	16.56	16.64	11.56	5.72	2.99

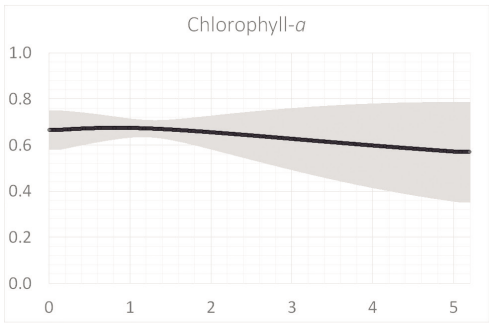
Dynamic oceanographic variables only contributed marginally to the development of annual models. The chlorophyll-a concentration, as an indicator of primary production, contributed only 7.79 ± 5.72% (Figure 2; Table 1) to the averaged model and the response curve showed a negative effect, with higher probability of Balearic shearwater presence at low levels of chlorophyll-a (< 1 mg m-3). The contribution of sea surface temperature was found to be minimal (3.20 ± 2.99%) and hardly showed any effect (Figure 2; Table 1).











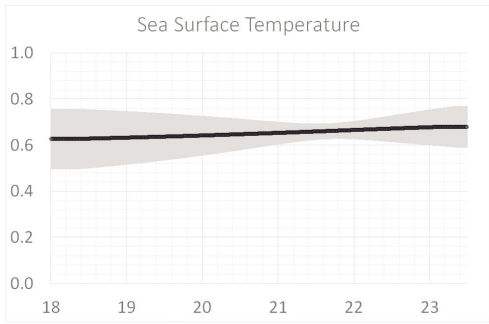


Figure 2. Averaged annual model response curve showing the predictors variables. The curves show the mean response of the 10 replicates Maxent runs over the 10 years dataset (black line) and the mean +/- standard deviation (grey).

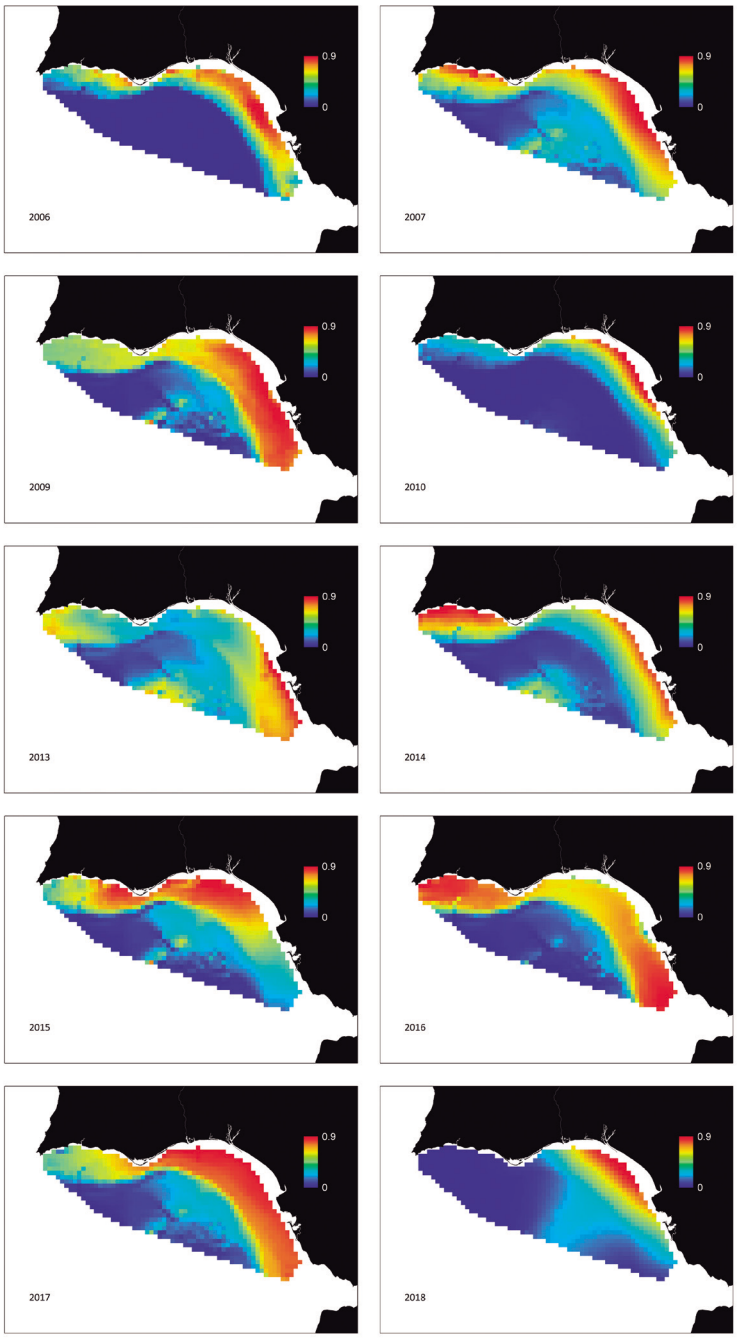


Figure 3. Representation of annual average 10 replicates Maxent model for the BSH in the GoC. Warmer colours show areas with better-predicted conditions.

Overall model

In order to analyse general distribution in the GoC and compare with annual models, an overall model was performed compiling the data over the 10 years of study. Thus, 63 models were tested, setting year as a random effect, and incorporating those variables with significant effects following a forward stepwise procedure (Table S4, supplementary material). Fourteen models showed statistically significant effects and are presented in the Table 2. Values of Moran Index were close to zero and significant in all cases, suggesting that spatial auto-correlation did not bias the results of the models.

When single predictors were considered (mod01 to mod06, Table 2), static features (bathymetry and distance to Guadalquivir river mouth) performed better than dynamic ones (CHL and SST). The most parsimonious and best fitting multivariate model (mod28, Table 2) also included SST, although the contribution of this variable with respect to the bivariate model (mod8, Table 2) was relatively small. According to the best fitting model, the probability of occurrence of Balearic shearwater decreases markedly towards deeper waters (primary fixed factor), as distance away from the mouth of the Guadalquivir river increases (secondary fixed factor) and also decreases as the sea surface temperature increase (tertiary fixed factor) (Figure 4). Any of the models that included the significant effect of CHL showed a poorer fit than those including the predictors described above.

Figure 5 shows the predicted optimal areas for the species during the summer in the GoC are found in shallow waters near the coast between the mouths of the Guadiana and Guadalquivir and extend towards Cadiz Bay. This pattern is consistent with the results obtained in the annual models (Figure 3).

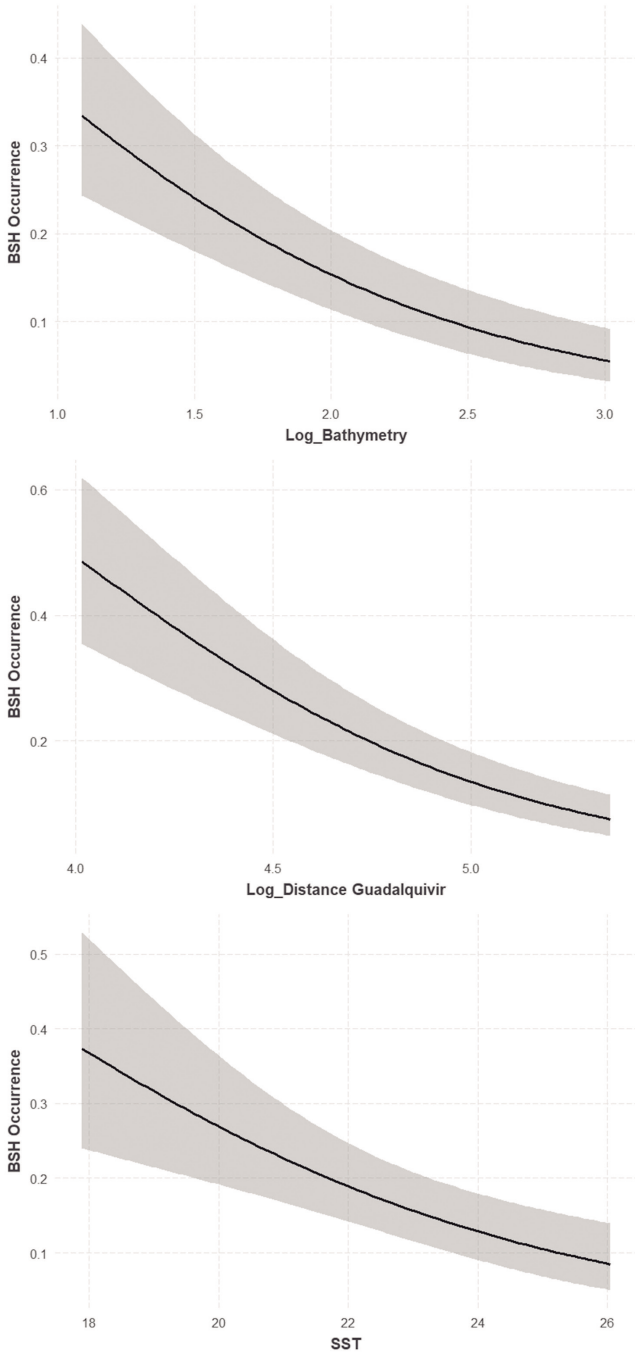


Figure 4. Representation of response curve illustrating relationship of occurrence prediction of BSH to main fixed factors in the best-fitted GLMM model. Grey shade shows 0.95 confidence intervals.

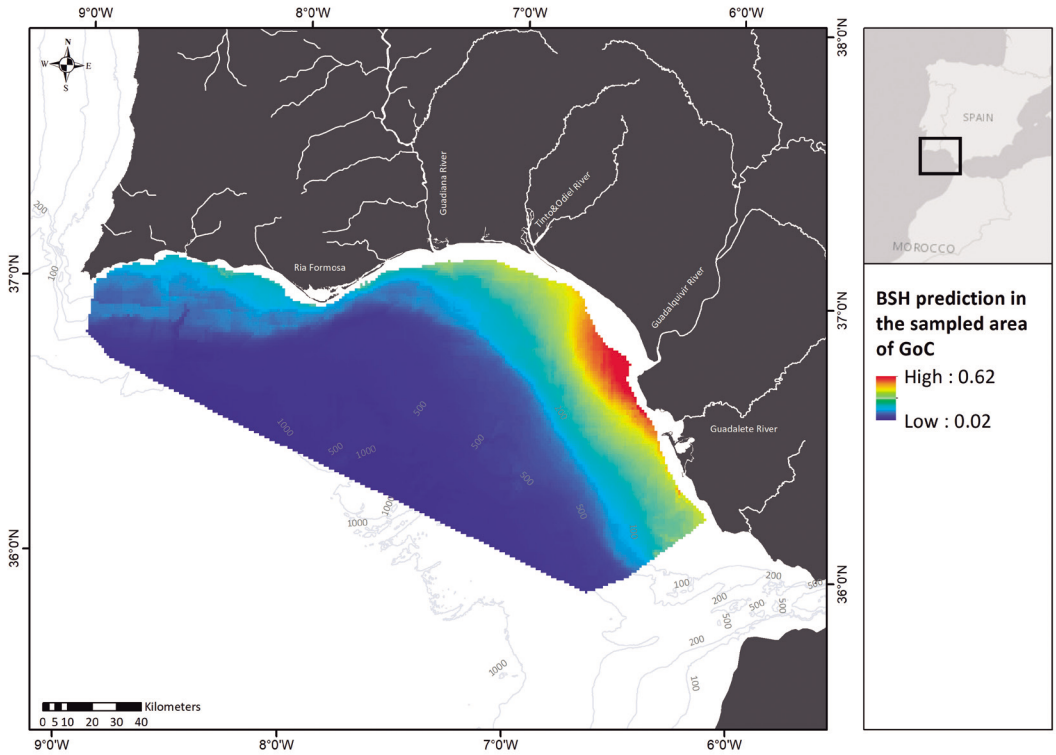


Figure 5. BSH occurrence prediction in the study area of the best-fitted GLMM exclusively on the sampled area.

Table 2. Biologically relevant explanatory variables used for Balearic shearwater overall distribution modelling and associated oceanographic processes. Shaded model (mod28) indicate the best model of the Balearic shearwater occurrence in the GoC. Only models with significant variables are presented in the table with their AIC (Akaike Information Criterion) value. ΔAIC delta represents the difference in AIC with respect to the best model. Moran index shows the spatial autocorrelation of the model residuals and p Value Moran index evaluate their significance. Distance variables are log-transformed, using logarithm base 10; bat indicates bathymetry in meters, d guadalq indicates the Euclidean distance from Guadalquivir river mouth in meters; CHL indicate chlorophyll-a concentration in mg m-3, iso200 indicate Euclidean distance from 200 m isobaths in meters; SST indicate the sea surface temperature in °C; df.resid: residuals of degrees of freedom.

#Model	Single variables	Estimate	Std. Error	p Value	deviance	df.resid	AIC	ΔAIC	Moran index	p Value Moran index
mod01	log_bat	-1.47	0.18	<0.001	1960.1	2108	1966.1	42.7	0.05	<0.001
mod03	log_guadalq	-1.75	0.21	<0.001	1964	2108	1970	46.6	0.04	<0.001
mod04	log_iso200	0.84	0.13	<0.001	1991.2	2108	1997.2	73.8	0.05	<0.001
mod05	CHL	0.29	0.09	0.00	2027.3	2108	2033.3	109.9	0.06	<0.001
mod06	SST	0.11	0.05	0.02	2031	2108	2037	113.6	0.05	<0.001
mod08	log_bat	-1.1	0.19	<0.001	1927.7	2107	1935.7	12.3	0.04	<0.001
	log_guadalq	-1.23	0.22	<0.001						
mod16	log_guadalq	-1.47	0.22	<0.001	1942.1	2107	1950.1	26.7	0.04	<0.001
	log_iso200	0.6	0.13	<0.001						
mod17	log_guadalq	-1.83	0.21	<0.001	1946.1	2107	1954.1	30.7	0.03	<0.001
	CHL	0.41	0.1	<0.001						
mod18	log_guadalq	-2.37	0.27	<0.001	1949.8	2107	1957.8	34.4	0.04	<0.001
	SST	-0.23	0.06	<0.001						
mod21	CHL	0.34	0.09	<0.001	2018.5	2107	2026.5	103.1	0.05	<0.001
	SST	0.14	0.05	0.00						
mod28	log_bat	-1.12	0.19	<0.001	1913.4	2106	1923.4	0	0.04	<0.001
	log_guadalq	-1.83	0.28	<0.001						
	SST	-0.23	0.06	<0.001						
mod38	log_guadalq	-1.59	0.22	<0.001	1935	2106	1945	21.6	0.03	<0.001
	log_iso200	0.46	0.14	0.00						
	CHL	0.28	0.1	0.01						
mod39	log_guadalq	-2.09	0.28	<0.001	1927.8	2106	1937.8	14.4	0.04	<0.001
	log_iso200	0.6	0.13	<0.001						
	SST	-0.23	0.06	<0.001						

Table 2. (Cont.)

#Model	Single variables	Estimate	Std. Error	p Value	deviance	df.resid	AIC	ΔAIC	Moran index	p Value Moran index
mod56	log_guadalq	-2.15	0.28	<0.001	1922.6	2105	1934.6	11.2	0.03	<0.001
	log_iso200	0.48	0.14	<0.001						
	CHL	0.24	0.1	0.02						
	SST	-0.21	0.06	<0.001						

DISCUSSION

Understanding how animals select their habitat and foraging resources therein is a crucial component of basic and applied ecology (Chudzińska *et al*., 2015). Prediction of species' distributions is central to diverse applications in ecology, evolution and conservation science (Elith *et al*., 2006). Particularly, when concerning species facing a high degree of global threat, distribution modelling may allow undertaking effective conservation strategies (Maiorano *et al*., 2019; Schank *et al*., 2019). The relatively long-term dataset analysed (including 10 years from a period of 13 years) accounts for some inter-annual variability (Tummon *et al*., 2015), whereas previous studies of the distribution of this species covered more limited time periods (Arcos *et al*., 2009; Louzao *et al*., 2012). Increasing the number of sampling years allowed an increased number of sampling units, thus providing the number of presences and absences needed to obtain better model performance with more reliable and robust results (Araújo & Guisan, 2006; Brotons *et al*., 2007; Meynard *et al*., 2019). Furthermore, since the choice of modelling method may influence the resulting predicted distribution (Araujo & New, 2007; Oppel *et al*., 2012), the predictions of two widely accepted methods of SDM, MaxEnt (Elith *et al*., 2011) and GLMM (Jamil *et al*., 2013) were combined. Both approaches provided similar and consistent results over time, supporting a relatively high confidence in the habitat selection pattern of Balearic shearwater in the GoC, thus increasing the relevance of this area for the conservation of this species (Araújo & Williams, 2000).

The results revealed the zone of the continental shelf with relatively shallow coastal waters in the vicinity of the Guadalquivir river mouth as the key area for the Balearic shearwater. Previous studies have showed that shallow waters close to the coast along the

Iberian continental shelf are suitable areas for the presence of Balearic shearwater (Louzao *et al*., 2006a) and this particular geographical pattern has been described recently (Arroyo el al., 2020). Their tendency to feed near coasts has been also studied (Arcos & Oro, 2002; Arcos *et al*., 2012), as well as their migratory movements closely following the Spanish Mediterranean coast (Mateos *et al*., 2010). Moreover, population concentrations close to large river mouths, in response to nutrient-loaded run-off, have also been reported for the species (Louzao *et al*., 2006a).

The association of Balearic shearwaters with the Guadalquivir estuary reflects the notably high biological productivity of this area (Ruiz *et al*., 2017). This highly altered estuary acts as a nutrient pump, where the high water turbidity constrains the primary production and, consequently, most of the nutrients reach the shallow shelf surrounding the Guadalquivir mouth (Caballero *et al*., 2014; J. Ruiz *et al*., 2017). These processes, together with warm temperatures during the summer period, maintains a persistently high chlorophyll concentration in these areas, while the rest of the shelf and the basin experience severe oligotrophic conditions (Navarro & Ruiz, 2006; Prieto *et al*., 2009). Moreover, the development and maintenance of phytoplankton blooms are strongly influenced by meteorological forces due to both the wind regime and episodes of high rainfall, which determine river discharges (Prieto *et al*., 2009). Thus, these nutrient-rich waters create a suitable environment for spawning and the subsequent development of the early life stages of pelagic fish species such as anchovy (*Engraulis encrasicolus*) (Catalán *et al*. 2006a, Ruiz *et al*. 2006), sardine (*Sardina pilchardus*) (Baldó *et al*., 2006) and several demersal fish species (Catalán *et al*., 2006) that constitute the main prey for Balearic shearwater (Louzao *et al*., 2006b; Käkelä *et al*., 2010).

There is a fairly large body of evidence that shows that areas of high chlorophyll-a concentrate a huge number of marine top predators, including predatory fish (Novianto & Susilo, 2016), cetaceans (Panigada *et al*., 2008; Gill *et al*., 2011; Breen *et al*., 2016) and seabirds (Weimerskirch *et al*., 2005; Louzao *et al*., 2012). Moreover, previous studies have succeeded in using CHL concentration as the main explanatory variable in the Balearic shearwater niche models (Louzao *et al*., 2006a; Louzao *et al*., 2012; Araújo *et al*., 2017). Chlorophyll may be indicative of the trophic linkage from phytoplankton to zooplankton and the small fish preyed upon by Balearic shearwaters. If high biological productivity is at the base of the recurrent use of this area by the species, why then are significant relationships not found with oceanographic variables connected to productivity and, in particular, with chlorophyll-a concentration?

The answer may rely on the fact that, in highly dynamic marine areas, the spatio-temporal lag between the phytoplankton blooms and its translation to the higher trophic levels of the food web can obscure the effect of chlorophyll on top predator occurrence (Croll *et al*., 2005; Pirotta *et al*., 2011). The plume of nutrients fertilizing the GoC from the Guadalquivir is displaced by the coastal currents as a function of the wind, turning from northwest to southeast (or vice versa) in a few days, with a prevalence of the eastward direction towards the Cape Trafalgar and the Strait of Gibraltar due to the predominance of westerly winds in the summer (García Lafuente & Ruiz, 2007; Gomiz-Pascual, 2017). This process has been estimated to take a period in the order of one or two weeks to reach the Trafalgar area (Gomiz-Pascual, 2017), causing a notable spatio-temporal decoupling between chlorophyll-a peaks and the availability of zooplanktivorous fish. This decoupling makes CHL a weakly effective tracer for the concurrent location of prey available for the Balearic shearwater. Moreover, the existence of a prominent point source of nutrients in the GoC would explain why a static variable like the distance to the river mouth becomes a better predictor than monthly averaged CHL in the model. Although the presence of Balearic shearwater appears to be more regular to the north of the Guadalquivir River estuary, it can be found across the whole sea area close to the estuary, tracking the fish-rich areas derived from the fertilization pulses around it.

In the best-fitted overall model, SST showed a marginal effect, with an increased probability of Balearic shearwater occurring in colder waters in the study area. This result appears to challenge the finding that warm and biologically productive waters near the Guadalquivir mouth are highly suitable for the reproduction of fish species such as the anchovy (Ruiz *et al*., 2006, 2009; Navarro & Ruiz, 2006). Moreover, the effect of intense easterly winds leads to lower water temperature and oligotrophic conditions, diverting early stages of anchovies away from favourable conditions (Ruiz *et al*., 2006). Further research is required to unravel the relationships between dynamic variables and Balearic shearwater prey availability. On the other hand, Balearic shearwater may exploit demersal fish available from trawl fishing (Arcos & Oro, 2002; Louzao *et al*., 2006b; Käkelä *et al*., 2010). GoC is a heavily exploited fishing area (Torres *et al*., 2013). Fisheries involve numerous trawlers, purse seiners and artisanal boats (Jiménez *et al*., 2004). Bottom trawl fishing provides substantial amounts of demersal prey to seabirds (Louzao *et al*., 2011a) and most of the fish discards are consumed by seabirds (Arcos & Oro, 2002). The association of Balearic shearwater with trawlers might also interfere with the local distribution patterns (Mateos & Arroyo, 2011).

This study reveals that, while in many cases primary productivity may be a good indicator of foraging areas for top predators, the decoupling in the translation processes across the different trophic links can break up this relationship, particularly in dynamic ecosystems like the GoC. Information about the immediate prey is generally scarce, however, focusing on this trophic linkage appears to be fundamental to advance the understanding of the distribution of marine predators.

Management and conservation implication

Techniques of environmental niche modelling for habitat selection are an essential management tool for conservation purposes in the marine environment, particularly to delineate core areas for conservation (Lascelles *et al*., 2016). Top marine predators are critical components in ecosystems as well as ecological indicators to identify and prioritize areas for conservation. They are generally long-lived, wide-ranging organisms that forage at high trophic levels, reflecting the influence of long-term and large-scale changes in ecosystems (Piatt & Sydeman, 2007; Rajpar *et al*., 2018). Changes in abundance and distribution of marine predators often result from alterations in the structure and function of the ecosystem (Springer *et al*., 2003; Estes *et al*., 2011; Siddig *et al*., 2016). Moreover, many of these marine top predators are vulnerable to cumulative impact of human activities such as fisheries' bycatch, emergent pollution or climate change, among others (Maxwell *et al*., 2013; Provencher *et al*., 2019; Trew *et al*., 2019).

The Balearic shearwater, one of the most globally threatened seabird species, is regarded as an umbrella species that can benefit from top-down conservation approaches (Ronconi *et al*., 2012; Siddig *et al*., 2016; Crawford *et al*., 2018). This and other seabird species are useful bio-indicators to assess disturbances in marine management (Furness & Camphuysen, 1997; Rajpar *et al*., 2018) and particularly, the Balearic shearwater is a priority in the European conservation plans, being legally protected across most of its distribution range in Europe. Its protected area covers waters off Spain, Portugal, France and the UK (Arcos, 2011). Species status was recently re-evaluated and ratified as 'Critically Endangered' by the IUCN Red List Committee due to the main threats remaining active (Genovart *et al*., 2016; IUCN, 2020b). With regard to this, the identification and assessment of the environmental factors driving Balearic shearwater distribution is key to underpinning an effective conserva-

tion strategy (Oppel *et al*., 2012; Araújo *et al*., 2017; Pérez-Roda *et al*., 2017). Our findings demonstrate that the spatial models of the Balearic shearwater and other seabirds based on primary production cannot be extrapolated to different regions due to the significant lag between this variable and processes more closely related to the distribution of the top predators, such as the presence of their prey (Fauchald, 2009). In this way, the general assumption of predicting the distribution of the endangered top predators based on primary productivity, could skew the prediction, relative to the actual distribution of the species and, therefore, the most appropriate area to be protected. In a recent article, it has been shown that the Special Protected Area (SPA) in the GoC, designated in 2014, does not match the key habitat of the Balearic shearwater, compromising its effective conservation (Arroyo *et al*., 2020). Our study adequately predicts the area with the highest probability of finding Balearic shearwaters in the GoC, which essentially coincide with the key area for the species described in Arroyo *et al*. (2020). This discrepancy highlights the need to expand the limits of the current SPA in the GoC to ensure the effective conservation of the species in one of the most important foraging areas during its migration.

To understand the mechanisms that drive the distribution of seabird species better, we must consider the complex oceanic processes and interspecific relationships that occur in the marine environment.

Chapter III

Predator-prey relationship reveals seabirds' spatial distribution in the Gulf of Cadiz

De la Cruz, A., Ramos, F., Tornero, J., Rincón, M., Jiménez, M.P. y Arroyo, G.M.

Under review in ICES Journal of Marine Science.

ABSTRACT

The biodiversity of marine ecosystems faces numerous conservation problems caused mainly by human activities and top marine predators are a good indicator of the environmental status of oceans. Determining what factors drive the distribution of marine predators is essential to predict changes in their populations and to anticipate future conservation problems. In this study, we explored the spatial relationships between top predators, such as seabirds, with their potential prey together with the environmental variables that determine primary production in a complex environment as the Gulf of Cádiz. For this purpose, space distribution models have been developed (GLM and GLMM) analysing seabird data obtained throughout the ECOCADIZ survey for the evaluation of the small pelagic fish stock. In general, the distribution of predators is more conditioned by the distribution of their prey than by other environmental variables. Particularly, for the critically endangered Balearic shearwater, the medium sizes of European pilchard and anchovy turned out to be the prey that determines their location. The sustainable management of these sources of food, such as fisheries, is essential in an effective maritime spatial planning that ensures the conservation of these apical marine predators.

INTRODUCTION

There is increasing evidence that the biodiversity of marine ecosystems is changing in response to climate change and human activity. Changes in the distribution of marine organisms can reflect such changes (Canonico *et al*., 2019). However, the vastness and inaccessibility of the ocean and the great dynamism and complexity of the marine environment make it difficult to understand the distribution patterns of marine biodiversity (Kaschner *et al*., 2006). Marine top predators are a critical indicator of changes in the marine environment, since they are usually more conspicuous and easy to monitor. Their movements cover wide ranges of the ocean and the changes in their distribution integrate alterations that occur at different levels throughout the marine food web, at different spatial and temporal scales (Hazen *et al*., 2019).

Recent advances in biomonitoring technologies and progress in remote sensing of the oceans provides a huge bulk of information on oceanographic features, which makes it possible to explore the relationships between oceanographic features and the occurrence of

the species (Reisinger *et al*., 2018). Some authors relate the presence of marine predators to abiotic factors, such as bathymetry, fronts or eddies (Louzao *et al*., 2009; Scales *et al*., 2014; De la Cruz *et al*. in press). On the other hand, other authors find the best drivers in biotic environmental variables such as large climate pattern changes or changes in primary production (Sprogis *et al*., 2018; Serratosa *et al*., 2020). However, in most cases, the distribution of top predators is determined by their food, in this case, the prey fish species they consume. In this sense, detecting clear and direct relationships between predators and prey is not that easy (Fauchald, 2009). Finding food resources is challenging for top-predators, due to prey distribution being patchy and unstable, and thus difficult to predict and locate (Bastos *et al*., 2020) and, therefore, few studies investigate relationships between marine predator and their prey (Serratosa *et al*., 2020). In this regard, to include more direct measures like food resource distribution would improve seabird model distribution (Kane *et al*., 2020). Moreover, direct relationships between marine predators and their natural prey may be masked by the appearance of alternative food sources, often coming from human activities, such as fishing discards, which has become a key food resource for many species and subsidises the food supply of a large community of seabirds (Depestele *et al*., 2016).

Among the different top marine predators, seabirds are the most conspicuous and relatively easy to study. Moreover, they are one of the most threatened groups of marine fauna, and their populations have experienced a severe decline in recent decades (Paleczny *et al*., 2015). Thus, there is an urgent need to identify and implement practical actions to deal with their threats (Dias *et al*., 2019). Recently, the development of acoustic methodology to measure the distribution and abundance of fish, has allowed the carrying out of joint surveys where the research of the predators of these fish species is possible from the same vessel (Sydeman *et al*., 2017). Determining the trophic relationships between marine predators and their prey is essential to identify what mechanisms drive their spatial distribution (Astarloa *et al*., 2019; Sadykova *et al*., 2020) and consequently, to achieve an assessment of the current situation and propose management measures. Within this context, the aim of this study was to analyse the relationships in the distribution of a set of seabird species (Cory's shearwater *Calonectris borealis*, Balearic shearwater *Puffinus mauretanicus*, European storm-petrel *Hydrobates pelagicus*, Northern gannet *Morus bassanus*, Audouin's gull *Ichthyaetus audouinii*) with their main potential prey in a highly dynamic area such as the Gulf of Cádiz. This information will provide useful knowledge and information for sustainable ecosystem-based management of their populations.

METHODS

Study area

The South-Atlantic Spanish Region (Subdivision 9a South of the ICES) is part of the Gulf of Cadiz, SW Iberian Peninsula (GoC hereinafter). This is a very dynamic area influenced by complex oceanographic processes (Sánchez-Leal *et al*., 2017), holding a very rich biodiversity related with its wide continental platform and the influence of intense run off of important rivers (Torres *et al*., 2013). These characteristics favour the upwelling of nutrients in the area and, therefore, fisheries of different target species and with different fishing gear proliferates (Jiménez *et al*., 2004). These important fishing areas are exploited not only by the fishing industry, but also by many seabirds, becoming a very important feeding area (Arroyo *et al*., 2020) accounting for five protected areas (marine SPAs) within the framework of the Natura 2000 network, being the most important marine area of Gulf of Cadiz (ES0000500).

In this context, this study was carried out in the framework of the annual ECOCADIZ acoustic-trawl surveys, conducted by the Spanish Institute of Oceanography (IEO) on board the R/V 'Miguel Oliver', between 2015 and 2019. This survey series is planned and coordinated following the protocols and standards recommended by the ICES Working Group of Acoustic and Egg surveys for small pelagic fish in NE Atlantic (WGACEGG; Massé *et al*., 2018). This survey took place every summer (late July until mid-August) from Cape Trafalgar (36.15°N, -6.02°W) in the Spanish side to Cape St. Vincent (36.97°N, -8.95°W) in the Portuguese side. The total area surveyed covers almost 8000 km^2 (Figure 1).

Seabird sightings

Seabirds were counted at one or two sides ahead of the vessel by an experienced observer using strip-transect techniques following the standard European Seabirds at Sea protocols (Camphuysen & Garthe, 2004), searching for seabirds ahead from the vessel within an angle of 180° from a platform located at 11 m above the sea level. Census were carried out under good weather condition and birds were recorded and summed up into 10 min survey units at a constant speed of 10 knots in order to obtain standardized data over the years. Although the exact number of seabirds in each detected sighting was recorded, the analysis performed were based on the species occurrence. This presence/absence was considered as the dependent variable (response) of the models.

Fish abundance estimates

Abundance of pelagic fish species (potential seabirds' prey) were estimated by following the protocol established in the ECOCADIZ survey design, which consists of parallel line transects, perpendicular to the isobaths and regularly spaced 8 nautical miles apart, from Cape Trafalgar to Cape St. Vincent and from the coast (20 m depth) to the 200 m isobath (Figure 1). Acoustic data were recorded en-route during the daytime while steaming at 10 knots along transects and at multiple frequencies (18, 38, 70, 120, and 200 kHz), using a Simrad EK60 hull-mounted split-beam echosounder (Kongsberg Simrad AS, Kongsberg, Norway), calibrated during each survey using a standard method (Demer *et al*., 2015). Raw data were post-processed using Echoview software package (Echoview Software Pty. Ltd.). Pelagic trawl hauls were performed adaptively during daytime at a towing speed of 4-4.5 knots, to inform on the relative species composition and biological parameters (length, weight, age, etc.) of fish echotraces. Thus, trawl hauls were performed on the positions of particular fish echotraces that are considered to be representative of similar echo traces observed elsewhere but not fished. The trawl gear used during ECOCADIZ was a 63.5/51 pelagic trawl, with a theoretical vertical opening of about 20-22 m, which does not exceed 10-15 m in practice. Fish acoustic densities were echo-integrated within 1 nautical mile (nm) long Elementary Distance Sampling Units (EDSU) along transects. Before echo-integration, virtual echograms referred to the 38 kHz frequency (i.e. the frequency used for biomass estimation) were generated based on multi-frequency algorithms (templates) to extract fish echotraces from other echoes (e.g., plankton, sound scattering layers). Regions including the fish echotraces were delineated along each EDSU in the echogram and allocated either to a single fish species (direct allocation based on expert judgment) or, more commonly, to multispecies aggregations, whose composition was given by the species composition of fishing hauls performed on similar echotraces in the area of interest (Nakken & Dommasnes, 1977). The resulting data after echo-integration are nautical area backscattering coefficients (NASC) (Maclennan, 2002) by species by EDSU along transects. After echo-integration, the spatial distribution for each species is analysed, taking into account both the NASC values and the positive hauls' length frequency distributions (LFD) to provide homogeneous assessment polygons (i.e. coherent post-strata). Within each polygon, differences in LFDs are tested using the Kolmogorov–Smirnoff (K–S) test. LFDs without significant differences are joined, providing homogeneous

LFD-based post-strata. Finally the species-specific NASC values within each post-stratum are further converted to abundance and biomass per species using the target strength and the mean weight by 0.5-cm size class of the species in the catch (Simmonds & Maclennan, 2005). This procedure results in estimating abundance (in thousands of fish) and biomass (tonnes) by size class per species for every EDSU along transects (more details can be found in Massé *et al*., 2018).

Each unit survey carried out to obtain seabird data was assigned the value of estimated fish abundance from the nearest EDSU after the acoustic evaluation.

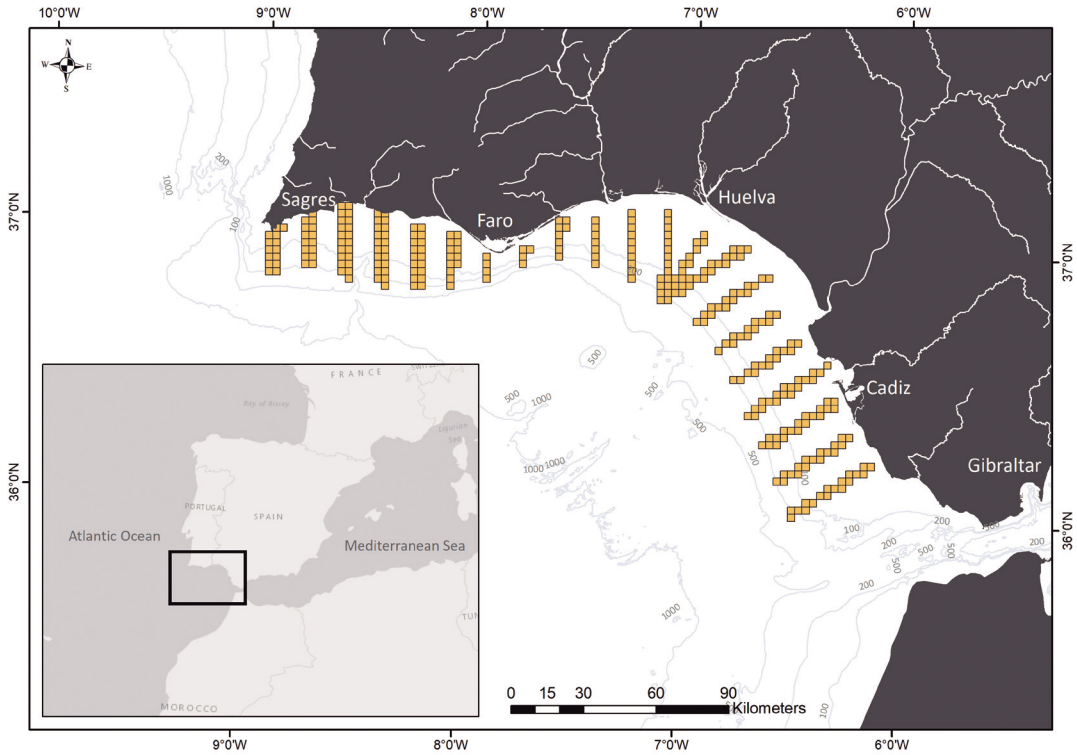


Figure 1. General map of the study area with an overview areas sampled during the ECOCADIZ surveys between the years 2015-2019. Isobaths of 100, 200, 500 and 1000 m are depicted.

Fish species and size selection

In order to avoid problems related to sample size (Wisz *et al*., 2008), only species that are present in at least 10% of the EDSUs (1 nm) were included in our models. Thus, we considered the following species: European anchovy *Engraulis encrasicolus* (ANE), European pilchard *Sardina pilchardus* (PIL), Atlantic mackerel *Scomber scombrus* (MAC), Chub mackerel *Scomber colias* (VMA), Atlantic horse mackerel *Trachurus trachurus* (HOM), Mediterranean horse mackerel *Trachurus mediterraneus* (HMM), Blue jack mackerel *Trachurus picturatus* (JAA) and Bogue *Boops boops* (BOG). Since seabird distribution can be determined not only by their prey species but also by its size (Tucker *et al*., 2016), the different species were classify in three sizes ranges categories following Arcos (2001), namely small size (0-99 mm), medium size (100-199 mm) and large size (≥ 200 mm). In addition, to test whether size is more important than species, three new categories by summing the abundances of all small, medium, and large species, were created.

Environmental variables description

We included demonstrated and relevant biotic variables such as sea surface temperature (SST), chlorophyll-a concentration (CHL), and turbidity (TSM; derived from reflectance following Caballero *et al*., 2014) as a proxy of primary production (Abdellaoui *et al*., 2017, McInnes *et al*., 2017). These dynamic oceanographic data were extracted monthly from Aqua MODIS satellite imagery via https://oceancolor.gsfc.nasa.gov/ at a spatial resolution of 4 x 4 km. When the sampling took place in two consecutive months, we calculated a new layer with the average value of both months.

Species distribution modelling construction

After testing collinearity between species (both predator and prey) and dynamic variables by pairwise Spearman-rank correlation test, not very highly correlated ($|rs| < 0.65$) pairs of variables were selected. When a pair of variables presented high correlation, the most ecologically relevant variable was chosen to be tested in the model, i.e. when two sizes of the same species were highly autocorrelated, smallest size was selected, since the small-size of pelagic fish is the basis of the diet of most of the bird species treated (Schreiber & Burger, 2001). Fish abundance presented a very large magnitude scale, so we used

log-transformed data in order to avoid convergence problems and scale variables bias (Schriver *et al*., 1995).

Generalized Linear Models (GLMs) using a binomial distribution and logit link function to examine simple relationships between response variables (seabird occurrence) and explanatory variables (year, oceanographic parameters and prey abundance) were used (Tremblay *et al*., 2009). When a year showed a significant value in the GLM, we ran a year variable as a random factor using a Generalized linear mixed model (GLMM) to control for possible temporal pseudo-replication (Millar & Anderson, 2004). Both model type, GLM and GLMM approach is widely used to identify species distribution and the relationship with the best explanatory variables (e.g., Tremblay *et al*., 2009; Jamil *et al*., 2013). Models were constructed for all possible combinations (Bartoń, 2019), however, in order to obtain more parsimonious models and whose biological explanation was not complex, only models with a maximum of two explanatory variables with lower AIC values were considered (Akaike, 1973; Burnham & Anderson, 2002).

Spatial autocorrelation model checking

Most of the species distribution data are spatially autocorrelated and modelling this type of data can invalidate the common assumption that observations are independent, and therefore obtain artificial or spurious significant relationships (Dormann *et al*., 2007). To deal with this issue, we calculated the Moran's I coefficient to assess the spatial autocorrelation patterns in the seabird data, which ranges from -1 (perfect dispersion) to +1 (perfect correlation), with zero values indicating random spatial patterns. When significant spatial autocorrelation was found in all residual models, this spatial autocorrelation structure was included to minimize its associated bias.

Model evaluation

Finally, to evaluate the predictive capacity of the best model, we used the area under the Receiver Operating Characteristic curve (AUC) (Pearce and Ferrier, 2000). AUC has been used extensively in the species' distribution modelling literature, to evaluate logistic regression models and assess the ability of a model to discriminate between sites where a species is present, versus those where it is absent (Russell *et al*., 2015). AUC is a threshold-indepen-

dent summary statistic that ranges from zero to one. An AUC of 0.5 indicates an unsuccessful model performance equal to a random prediction, whereas values from 0.5 to 1 with the following model predictive performance classification: 0.9 excellent, 0.9–0.8 good, 0.8–0.7 reasonable, 0.7–0.6 poor (Engler *et al*., 2004).

Spatial distribution overlapping

In order to estimate the home range for all considered species (seabirds and fishes), we calculated the 50% (key area) and 95% (home range) utilization distribution contours (UDC 50, UDC 95) from their presence using the kernel density estimation (KDE) analysis (O'Brien *et al*., 2012). Then, we calculated the overlap degree of the distributions between predators and preys by means of the Volume of Intersection Index (VI) (Seidel, 1992), as a statistical measure of overlap between the distributions following Fieberg (2014). This VI index takes values from zero to one, where zero means no overlap and one means total overlap and identical distribution.

Implementation

All analyses were performed using R software (R Development Core Team, 2020). GLM was ran using glm R function from 'stats' package (R Development Core Team, 2020) and GLMM was ran using glmer R function from the 'lme4' package (Bates *et al*., 2015). Home range (UDC Contours) was calculated using kernel density analysis from adehabitatHR R package (Calenge, 2006) and Volume of Intersection Index was calculated using Home range overlap indices from KernSmooth package (Wand & Ripley, 2015). Model selection was performed using dredge function, and Receiver Operating Characteristic curve using AUC function, both of the R package 'MuMIn'. Moran's I coefficient was calculated using Moran.I R function from 'ape' library (Paradis *et al*., 2004).

RESULTS

Fish species composition and distribution

Fifteen different species of fish were evaluated during the fishing operations. Of these, eight species were selected as they accounted for more than 10% of the total catches. European pilchard and European anchovy were the two most abundant species with more than one million average individuals for each sample unit. Chub mackerel also showed relatively high abundances during the surveys with more than two hundred thousand individuals on average per sampled unit. The last was also the most widely distributed species, occurring in more than 70% of the sampled units, followed by sardine, anchovy and bogue, all of them present in more than half of the total sampled units (Table 1).

Table 1. Fish species considered in this study to exceed 10% of the annual abundance showing their frequency of presence and their average abundance (x1000) per evaluated mile. SD: Standard deviation (x1000). SMA: small size (<99 mm), MED: medium size (100-199 mm) and LAR: large size (>200 mm).

Fish species and size	Occurrence percentage	Mean abundance (x1000)	SD (x1000)
European pilchard _MED	64.39%	1297.94	9460.26
European anchovy _MED	66.81%	1107.53	4041.10
European anchovy _SMA	19.74%	234.07	1679.98
Chub mackerel _MED	60.42%	143.95	1016.97
Chub mackerel _LAR	71.00%	84.68	556.63
Atlantic horse mackerel _LAR	41.57%	17.98	128.70
Atlantic mackerel _MED	14.77%	15.03	214.10
European pilchard _SMA	22.49%	14.47	144.07
Mediterranean horse mackerel_LAR	24.48%	13.97	77.49
European pilchard _LAR	17.75%	11.40	147.57
Blue jack mackerel _MED	28.00%	9.52	98.36
Atlantic horse mackerel _MED	41.57%	9.08	57.58
Blue jack mackerel _LAR	21.50%	8.24	99.96
Bogue_LAR	51.38%	4.51	29.40
Atlantic mackerel _LAR	45.09%	3.04	21.78
Atlantic horse mackerel _SMA	10.47%	0.19	2.47
Bogue_MED	28.22%	0.16	1.28
Mediterranean horse mackerel_MED	3.75%	0.01	0.15

All considered fish species were distributed throughout the entire study area (UDC 95), with the exception of the Blue jack mackerel, which was restricted to the western sector, and the Mediterranean horse mackerel, which, on the contrary, was distributed in the eastern zone of the GoC (Figure 2). Moreover, most of the species showed a similar key area (UDC 50) of their smaller and larger sizes, except anchovy, sardine, and Mediterranean horse mackerel (Figure 2). Both anchovies and sardines concentrated their home range of their small sizes in front of the mouths of the large rivers (Guadiana and Guadalquivir), while their medium sizes moved to the west (Figure 2, A and B). On the other hand, Mediterranean horse mackerel presented the home range of its smaller size (medium-size) and larger (large-size) in a patched way (Figure 2, G).

Seabird distribution patterns

We conducted 907 survey units for counting seabirds between 2015 and 2019. Overall, Cory's shearwater was the most abundant seabird with presence in 58.99% of the surveyed units. Northern gannet and Balearic shearwater were detected in 32.52% and 22.05% of the surveyed units, respectively. Both European storm-petrel and Audouin's gull occurred in less than 7% of the surveyed units (Table 2).

Cory's shearwater and Northern gannet were the most widely distributed species, occupying almost the entire study area (Fig. 3. A and D). Balearic shearwater concentrates its UDC 50 in the eastern part of the GoC, between the Spanish-Portuguese border and the Bay of Cádiz (Fig. 3. B). European storm-petrel showed three distribution nuclei where its UDC 50 is included, one on the western margin of the GoC, another on the border between Spain and Portugal and the last one on the south-eastern side of the study area, all far from coast (Fig. 3. C). Finally, Audouin's gull restricted its key distribution area to the central area of the GoC (Fig. 3. E).

Table 2. Seabird occurrence, number of survey units where the different species of seabirds considered in this work appear each year.

Species/season	2015	2016	2017	2018	2019
Cory's shearwater	98	47	149	124	117
Balearic shearwater	42	17	86	27	28
European storm-petrel	10	5	26	19	3
Northern gannet	47	13	92	71	72
Audouin's gull	11	0	12	18	20
Total survey units	**152**	**138**	**246**	**165**	**206**

Spatial autocorrelation

Since a positive, albeit weak, significant spatial autocorrelation was found in all residual models except the Cory's shearwater and European storm-petrel model, we included a spatial autocorrelation structure into the models. After applying the spatial structure, some results still indicate a positive spatial autocorrelation. However, the value of the Moran index after including the spatial structure in the models become almost zero, which means random spatial patterns, and therefore no biases related to this problem are expected in the models (Table 3).

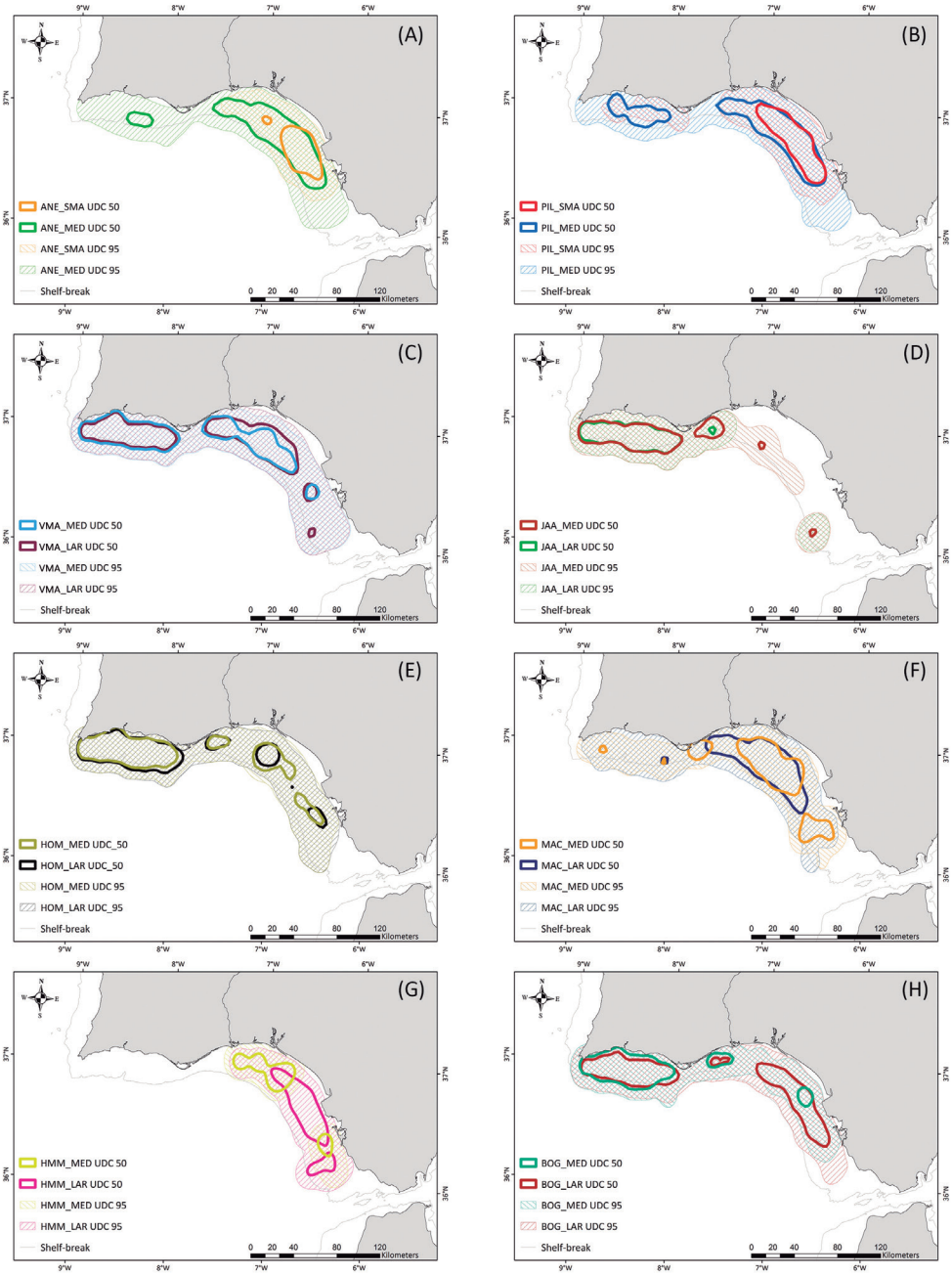


Figure 2. Distribution of considered fish species in this study. UDC 95 shows its home range and UDC 50 shows its core area. SMA: small size (<99 mm), MED: medium size (100-199 mm) and LAR: large size (>200 mm). ANE: European anchovy *Engraulis encrasicolus*; PIL: European pilchard *Sardina pilchardus*; MAC: Atlantic mackerel *Scomber scombrus*; VMA: Chub mackerel *Scomber colias*; HOM: Atlantic horse mackerel *Trachurus trachurus*; HMM: Mediterranean horse mackerel *Trachurus mediterraneus*; JAA: Blue jack mackerel *Trachurus picturatus*; BOG: Bogue *Boops boops*.

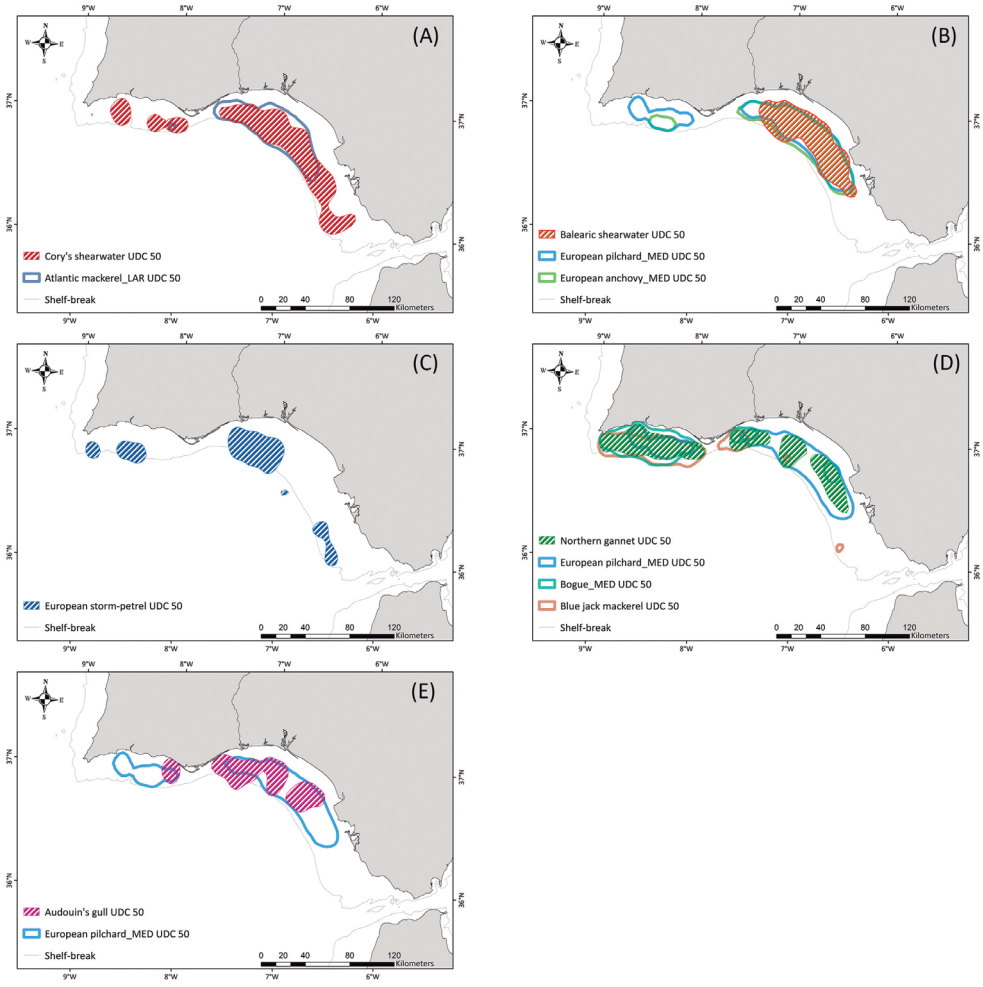


Figure 3. Core area range distribution (UDC 50) of seabirds and fish species considered in this study that show positive and significant relationships in the analysed models. Note that European storm-petrel does not show any positive relationship with any fish species.

Table 3. Best explanatory models obtained to model the distribution of the different species of seabirds considered. Only models with significant variables are presented in the table ordered by AIC (Akaike's Information Criterion) value. LN_ means natural logarithm of the abundance of the different species of fish considered. Year only apply as random effects in GLMM models. GLMM-PQL applied when spatial structure is applied in order to minimize autocorrelation bias. CHL indicate chlorophyll-a concentration in mg m-3. SST indicate the sea surface temperature in °C. df.resid: Residuals degrees of freedom. Moran I indicates the degree data over-dispersion or aggregation p Moran I indicates its statistical significance.

			Random effects (YEAR)								
Seabird's species	**Model type**	**Estimated parameters**	**Variance**	**Std. Dev**	**df**	**Moran I**	**p Moran I**	**AIC**	**ΔAIC**	**Deviance**	**AUC**
Cory's Shearwater	GLMM	*null model*			1			1193.5	0	1189.5	
		0.519 - 0.087 LN_BOG_MED - 0.040 LN_HMM_LAR	0.32	0.57	4	0.01	0.22	1186.7	-6.8	1178.6	0.67
		0.312 - 0.084 LN_BOG_MED + 0.039 LN_MAC_LAR	0.31	0.55	4	0.01	0.14	1187.5	-6	1179.5	0.66
		0.226 + 0.040 LN_MAC_LAR	0.29	0.54	3	0.01	0.14	1191	-2.5	1185	0.64
Balearic Shearwater	GLMM-PQL	*null model*			1			930.6	0	926.6	
		- 1.520 - 0.086 LN_MAS_MED + 0.076 LN_PIL_MED	0.272	0.52	4	0.02	0.00	894.1	-36.5	886.1	0.71
		- 1.566 + 0.064 LN_ANE_MED - 0.077 LN_VMA_MED	0.257	0.51	4	0.03	<0.001	896.2	-34.4	888.2	0.71
		- 2.490 + 0.055 LN_ANE_MED + 0.075 LN_HMM_LAR	0.248	0.50	4	0.03	<0.001	898.4	-32.2	890.3	0.70
		- 1.638 + 0.077 LN_ANE_PEQ + 0.256 LN_HMM_MED	0.115	0.34	4	0.03	<0.001	899	-31.6	891	0.69
		- 1.957 + 0.060 LN_HMM_LAR + 0.051 LN_PIL_MED	0.260	0.51	4	0.03	<0.001	902.3	-28.3	894.2	0.7
European Storm-petrel	GLMM	*null model*			1			449.6	0	445.6	
		- 2.356 - 0.217 LN_ANE_PEQ - 0.379 LN_BOG_MED	0.683	0.83	4	0.01	0.22	418.1	-31.5	410.1	0.78
		- 1.984 - 1.41 CHL - 0.211 LN_ANE_PEQ	0.451	0.67	4	0.01	0.24	424.7	-24.9	416.7	0.76
		- 2.064 - 0.086 LN_ANE_MED - 0.338 LN_BOG_MED	0.688	0.83	4	0.02	0.01	427.7	-21.9	419.6	0.76
		- 2.488 - 0.182 LN_ANE_PEQ - 0.099 LN_HMM_LAR	0.615	0.78	4	0.01	0.07	428	-21.6	420	0.76
		- 2.287 - 0.052 LN_ANE_MED - 0.178 LN_ANE_PEQ	0.603	0.78	4	0.02	0.01	428.1	-21.5	420.1	0.76

Table 3. Cont.

			Random effects (YEAR)								
Seabird's Species	**Model type**	**Estimated parameters**	**Variance**	**Std. Dev**	**df**	**Moran I**	**p Moran I**	**AIC**	**ΔAIC**	**Deviance**	**AUC**
Northern Gannet	GLMM-PQL	*null model*						1114.4	0	1110.4	
		- 1.658 + 0.474 CHL + 0.600 LN_PIL_MED	0.359	0.60	4	0.02	0.00	1072.2	-42.2	1064.2	0.71
		- 1.477 + 0.137 LN_BOG_MED + 0.604 LN_PIL_MED	0.427	0.65	4	0.04	0	1075.1	-39.3	1067	0.69
		- 1.381 + 0.518 CHL + 0.152 LN_BOG_MED	0.357	0.60	4	0.01	0.06	1075.6	-38.8	1067.6	0.71
		-2.593 + 0.810 LN_PIL_MED - 0.175 SST	0.38	0.61	4	0.03	<0.001	1075.7	-38.7	1067.7	0.69
		- 1.599 + 0.690 LN_JAA_MED + 0.770 LN_PIL_MED	0.418	0.65	4	0.03	<0.001	1078	-36.4	1070	0.69
Audouin's Gull	GLM-PQL	*null model*			1			449.1	0	447.1	
		- 3.359 + 0.076 LN_PIL_MED	NA		2	0.02	0.00	437.5	-11.6	433.5	0.64
		- 2.852 + 0.387 CHL	NA		2	0.03	<0.001	447.1	-2	443.1	0.61

Modelling occurrence probability

After the collinearity inspection, 10 out of 29 variables considered in the Spearman test showed high autocorrelation (>0.65) (Table S1). Water turbidity (TSM) and chlorophyll a concentration (CHL) showed the highest autocorrelation (0.8), and the species Bogue, Atlantic horse mackerel, Blue jack mackerel and Chub mackerel showed a high correlation (0.70-0.78) between their medium and large sizes. No relationship higher than 0.39 was found between any species of fish or seabirds with CHL or SST (Table S1 and Figure 2, 3 and 4). Likewise, no species of seabird showed autocorrelated values among them (max. 0.16). On the other hand, the general small-sized fish group is highly correlated with the small anchovy (0.79), the medium-size fish with sardine and anchovy (0.69) and the large-sized fish group is also highly correlated with large-sized Atlantic mackerel (Table S1 and Figure 2).

According to AUC, best fitting modes are depicted in Table 3. Most models including prey (fish) species predicted better the predator distributions than those including oceanographic variables such as SST and CHL (Table 3). European storm-petrel and Balearic shearwater models presented the best predictive performance with an averaged AUC of 0.762 ± 0.011, and 0.703 ± 0.009 respectively, which means a moderate to good discrimination. Best Balearic shearwater models output indicate a higher probability of occurrence when medium-sized anchovies and sardines occurred in the area. Four out of five best models included one of these medium-sized species. On the other side, medium-sized Mediterranean horse mackerel showed a positive relationship in three out of the five best models (Table 3, Figure 3, C).

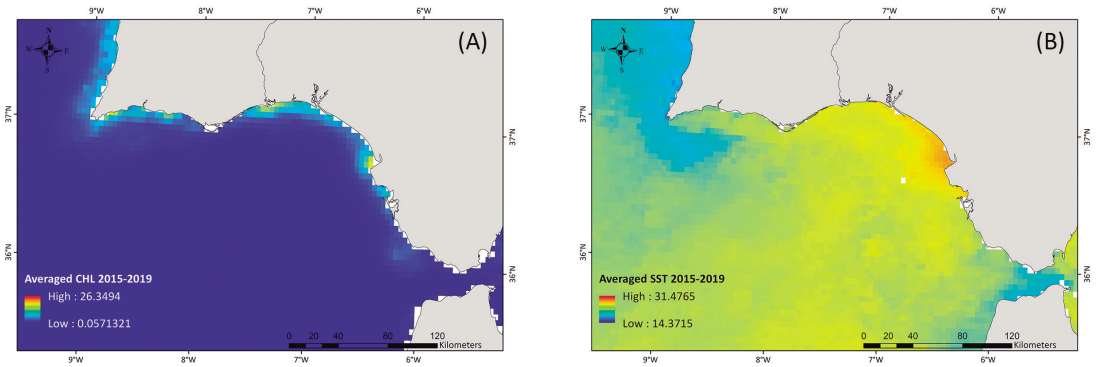


Figure 4. Average values of chlorophyll-a concentration CHL (mg·m-3) (A) and sea surface temperature SST (°C) (B) along the considered years (2015-2019).

European storm-petrel distribution showed a negative and significant relationship with the medium and small size of European anchovy and the medium size of Bogue (Table 3, Figure 3, E).

The Northern gannet model showed a moderate predictive performance, with an average AUC value of 0.696 ± 0.011. Its distribution seemed to be conditioned by medium-sized sardines, showing significant and positive relationships in four of the five best models. Moreover, CHL and medium-sized Bogue also present positive relationships in the two best models (Table 3 and Figure 3, B). On the other hand, Cory's shearwater and Audouin's gull failed to provide a good prediction model with a mean AUC of 0.654 ± 0.011 and 0.625 ± 0.026 respectively (Table 3).

Overlapping between predator and prey distribution

The VI analyses shows that the distributions of the predator-prey species with a positive relationship are overlapped always more than 39%, while the negative ones are below 32% (Table 4). Balearic shearwater shows the best overlap, sharing 71% with the distribution of the medium-sized anchovy and 65% with the medium-sized sardine (Figure 3, B). Northern gann*et* also overlaps 62.6% with medium-sized sardine, whereas storm petrels distribution shows weak and negative relationship with the coastal fish species, like anchovies and bogues.

Table 4. Volume of Intersection Index (VI) in percentage of overlap of the home ranges of the different seabirds and fishes considered whose relationship is significant in their best models. In the column 'Relationship' it is indicated when the applied model shows a positive or negative relationship.

Seabird species	Fish species	VI 50%UDC	Relationship
Cory's shearwater	Bogue_MED	0.3	-
	Atlantic mackerel _LAR	0.58	+
	Mediterranean horse mackerel_LAR	0.26	-
Balearic shearwater	European anchovy _MED	0.71	+
	European pilchard _MED	0.65	+
	Chub mackerel _MED	0.25	-
	European anchovy _SMA	0.39	+
	Mediterranean horse mackerel_LAR	0.42	+
	Mediterranean horse mackerel_MED	0.47	+
European storm-petrel	European anchovy _SMA	0.02	-
	Bogue_MED	0.31	-
	Mediterranean horse mackerel_MED	0.05	-
Northern gannet	Bogue_MED	0.61	+
	European pilchard _MED	0.63	+
	Blue jack mackerel _MED	0.61	+
Audouin's gull	European pilchard _MED	0.50	+

DISCUSSION

Marine top predators are known to concentrate their foraging areas in specific oceanic locations with abundant prey (Green *et al*., 2020). However, revealing relationship between predators and their prey is not an easy task (Fauchald, 2009). Moreover, information on predator-prey distribution are rarely available and usually hard to obtain (Astarloa *et al*., 2019). Alternatively, the increasing development of satellite remote sensing has allowed the revelation of the relationships of marine predator distributions with dynamic features of the ocean, like primary productivity and sea surface temperature (Polovina *et al*., 2004; O'Toole *et al*., 2017; Zainuddin *et al*., 2017).

The obtained results support that, in the Gulf of Cadiz, the occurrence of top predators, such as seabirds, are more driven by the distribution of their prey than by indirect proxies like primary production. The results of our best models indicate more consistent predator-prey relationships than predator-environmental variables ones. Furthermore, the distribution neither of the seabird nor of fish species showed high autocorrelation with the parameters related to primary productivity. This finding supports that, in dynamic marine ecosystem, the spatio-temporal decoupling in the translation processes across the different trophic links can break up these spatial relationships (De la Cruz *et al*., in press). The best example is found in the Balearic shearwater. Its distribution has been generally associated to the chlorophyll-a concentration throughout its distribution range (David *et al*., 2011; Martín *et al*., 2020). However, in highly dynamic oceanographic areas, as the GoC, we did not found any correlation of the species distribution to areas of high chlorophyll-a concentration (De la Cruz *et al*., in press.). When the distribution of prey species on which it feeds, namely pelagic fish (Arcos & Oro, 2002; Käkelä *et al*., 2010), is incorporated in the analysis, their occurrence has revealed to be clearly associated with schools of sardines and/or anchovies and their distribution highly overlap.

On the other hand, significant relationships are not always revealing direct predator-prey links. This is the case of European storm-petrel, that feed on small fish and mainly krill (Albores-Barajas *et al*., 2011), which were not a target species of the acoustic evaluation carried out during the ECOCADIZ surveys. The negative relationships of its best models can be interpreted as a divergent distribution of European storm-petrel towards deep waters away from the coast, compared to a coastal distribution of anchovies and bogues. Similarly,

the pelagic distribution of the storm petrel appears further away from the coastal areas that show higher values of primary production, which would explain the negative relationship with chlorophyll-a.

The spatial distribution of northern gannet showed a moderate relationship and a reasonable overlap with potential natural preys, namely medium sardines and bogues. Northern gannets exhibit a wide range of diet based on medium sized pelagic fishes and even squids, and since they are a regular scavenger attending trawlers in some parts of their range (Votier *et al*., 2013), this behaviour could mask the performance of their best models.

In the case of Cory's shearwater, which can be found virtually anywhere throughout the study area, the distribution models failed to reveal consistent relationships. This is the most abundant species in this area, where they occur in large figures during migratory periods for feeding (De la Cruz, 2013). They feed on a large group of pelagic fish (Reyes-González & González-Solís, 2016) and are often attracted by discards from trawlers (Louzao *et al*., 2009) making it difficult to find a distinctive drive in its distribution. In addition, during summer both *Calonectris* species, Cory's shearwater (*C. borealis*) and the Mediterranean Scopoli's shearwater *C. diomedea,* (difficult to discriminate at distance), coincide in the GoC (Flood & Gutiérrez, 2019) and this co-occurrence could also make it difficult for a species-specific pattern to appear.

The distribution of Audouin's gull coincides with the main fishing areas of the trawling fleet in the GoC, and consequently the largest amount of fish is caught and discarded in this area (Gamaza-Márquez *et al*., 2020). Audouin's gull is undoubtedly one of the species best adapted to foraging on discards provided by trawlers (Oro & Ruxton, 2001), and it is predictable that the number and location of trawlers will better determine their distribution.

Implications of the management and conservation of the fishing grounds

Unraveling when and where species are found and what variables determine their occurrence is essential to understanding the functioning of an ecosystem (Critchley *et al*., 2018). It is clear that top predators distribution is not driven by a single element and multiple factors will determine where we can find them (Fauchald, 2009). The obtained results support that prey location is undoubtedly essential information to understand the distribution of the top predators. Therefore, in our case study, the appropriate evaluation and management of fish stocks will be essential to achieve the conservation of these seabird species.

The Marine Strategy Framework Directive (MSFD) aims to achieve Good Environmental Status (GES) in European Union waters by 2020 (MSFD, 2008/56/EC), through improved management, based on supporting state indicators. GES of EU waters is being assessed based on indicators collected in all EU regional seas, within the framework of national monitoring programs. For cost-efficiency reasons, these monitoring programs have been developed by extending existing monitoring activities (Shephard *et al*., 2015). In this sense, the coupling of fishery evaluation surveys with marine predator surveys can be a suitable and cost effective approach to deal with this issue, and may provide essential information for an Ecosystem Based Management of the fisheries. Thus, the ECOCADIZ acoustic-trawl survey, conducted since 2004 in the GoC Cadiz, has been conceived as an integrated ecosystem survey, from physical oceanography to top predator ecology (Doray *et al*., 2018). This campaign, in addition to providing a regional index for the assessment of the southern component of the anchovy and sardine stocks in the 9th ICES division, has become a holistic monitoring program of the GoC pelagic ecosystem. Moreover, this survey represents a unique opportunity to explore the long term variability of species relationships to their habitats in a diversified food web. ECOCADIZ fulfils MSFD requirements by collecting observations and deriving potential indicators of the state of the GoC pelagic ecosystem in summer, thus providing fundamental information for an Ecosystem-Based Management of fisheries.

Worldwide, the growth in fish consumption reached historical maximum catches at sea in 2018 with more than 84 million tonnes, the group of small pelagic fishes being the most important among them (FAO, 2020). These small pelagic fishes, such as anchovies and sardines, are the basic diet of the many top predators (Certain *et al*., 2011) and, in general, their fishing grounds have alarming biomass levels below biologically sustainable thresholds (FAO, 2020). In our study area, sardine catches have radically drop in the last 40 years (ICES, 2020a). Although the current assessment of sardine stock indicates they are above the threshold of the maximum sustainable yield (MYS), its level is so close to the risk threshold that it is inadvisable to increase the catch quota for the year 2020 (ICES, 2020a). On the other hand, the European anchovy stock in the GoC (southern zone of the 9th division ICES) has remained somewhat more stable in recent years, although showing a negative trend in the last decade (ICES, 2020b) with notable fluctuations (ICES, 2019). Recent predictive models in the GoC show the current management system for small pelagic with fixed total allowable

catch (TAC), such as the European anchovy, compromises the sustainability of this fishery (Ruiz *et al*., 2017). This decrease in the fish population in the study area can be expected to produce negative effects at higher trophic levels on the species that depend on this resource, compromising their survival (McClatchie *et al*., 2018).

There are many examples where the overexploitation of fishing resources has had dramatic consequences on the species that depend on them (Frederiksen *et al*., 2004; Okes *et al*., 2009; Drago *et al*., 2018). However, the sustainable management of fisheries through marine protected areas can provide a wide range of benefits, increasing the biodiversity of the fishing ground and improving its productivity (Hyrenbach *et al*., 2000; Hooker & Gerber, 2004). Furthermore, the alternative food provided by the fishery through discards is widely used by a large group of seabirds (Sherley *et al*., 2020). Approximately 3,500 tonnes of fish are discarded each year in the GoC, accounting for ca. 34% of the total catch (Gamaza-Márquez *et al*., 2020). Therefore, the measures to discards ban and Landing Obligation (European Union Regulation 1380/2013) will bring unknown consequences after this food source suppression that may affect predators' conservation.

In this sense, the GoC hosts several seabird species throughout the year, including the critically endangered Balearic shearwater (De la Cruz, 2013). This species visits the study area during its migratory periods in search of small pelagic fish. To promote the conservation of seabirds such this and other species considered in this study, in 2013 the SPA Gulf of Cadiz (ES0000500) was declared as part of Natura 2000 network. Recently, an extension of the boundaries of this protected area has been proposed, to encompass the entire key distribution area (Arroyo *et al*., 2020). We have demonstrated that this key area highly overlaps with the main distribution areas of prey. The designation of this marine SPA must be accompanied by conservation measures that respond to the ecological requirements of the types of natural habitats and species present in these areas. The results of this study highlight the relevance of promoting best practices towards sustainable fisheries management to guarantee the conservation of seabirds in this key area of their distribution.

Chapter IV

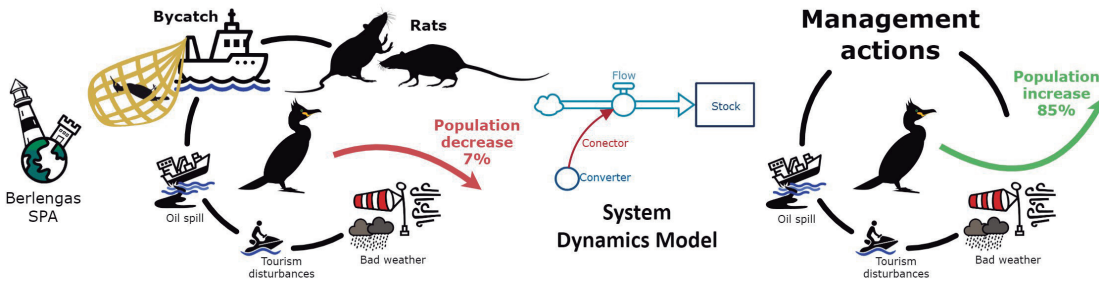
What to expect from alternative management strategies to conserve seabirds? Hints from a dynamic modelling framework applied to an endangered population

De la Cruz, A., Bastos, R., Silva, E., Cabral, J.A. y Santos, M.

Under review in Animal Conservation.

ABSTRACT

Seabirds declining worldwide due to the combined effects of global and regional changes are creating immense challenges for managers and conservationists. Predicting population responses to projected management strategies could support the most effective ones to prevent, halt and reverse ongoing declines. System dynamic modelling frameworks are considered particularly relevant to interrelate biological, ecological and environmental characteristics and envisage population trends. A system dynamics model was designed, compiling disperse information concerning a relict population of the European Shag located in western Iberia, to outline the best management options for the species' conservation. The simulations obtained seem to demonstrate that the presence of invasive mammals and bycatch mortality are the main reasons for the current population decline. Without management, a decrease of 7% is predicted for the next decade, which could be upturned by specific conservation actions. The results obtained show the usefulness of dynamic modelling frameworks to understand local cause-effect relations and species responses to ecosystems' management under changing environmental conditions. We highlight that the framework proposed, after specific parameterisation, could be easily adaptable to other species within similar socio-ecological systems.



Graphical abstract with the main ecological and anthropogenic factors considered affecting European Shag population dynamics.

INTRODUCTION

Seabirds face complex and multiscale conservation challenges, such as breeding habitat loss, rapid decline of their prey populations, overfishing and water pollution (Croxall *et al*., 2012; Dias *et al*., 2019). Furthermore, low reproduction rates and late sexual maturity contribute to the imperilled conservation status of many species, threatening the keystone roles played by these predators in marine ecosystems (Hall *et al*., 2000; Tam *et al*., 2017). Moreover, seabirds are highly mobile, cover large areas and depend on diverse resources triggered by ecosystem dynamics (C. Lambert *et al*., 2017a). Therefore, species have been relatively well-monitored and used for evaluating the ecological status of marine environments, namely for detecting changes in fish stocks and the impacts of oceanographic events (Furness & Camphuysen, 1997; Paleczny *et al*., 2015; Provencher *et al*., 2019).

The conservation and management of threatened species is embedded in realistic demographic parameters, essential to foresee trends of populations when management actions are applied (S. Lambert *et al*., 2018). Besides, the diagnose of anthropogenic pressures involves an understanding of life history and how parameters change with environmental stochasticity (Lande *et al*., 2003). To address this problematic, Population Viability Analysis (PVA) has been extensively used, particularly to predict the extinction risks of threatened species (Morris & Doak, 2002). However, PVA are typically limited to demographic and environmental stochasticity and habitat loss and, while inclusion of other factors is often possible, involves simplifying relevant interactions and their likely effects (Bennett *et al*., 2019; Lucas, 2020). In this way, some authors recommend developing tailor-made applications for the particular purpose and data available (Bennett *et al*., 2019; Lucas, 2020). In this perspective, dynamic modelling frameworks underpinned by bio-ecological information are specially welcomed (Anderson *et al*., 2018; Miller *et al*., 2019). In fact, dynamic modelling is currently considered a fundamental tool in ecology, by merging scattered information within a common and understandable framework, in addition to predicting the future consequences of alternative management scenarios (Warwick-Evans *et al*., 2016; Weller *et al*., 2016). Several types of dynamic models have been used to evaluate and predict the outcome of contrasting scenarios in the scope of conservation ecology (Banos-González *et al*., 2016; Morinha *et al*., 2017; Li *et al*., 2020). System Dynamics (SD) has been considered particularly useful, by its straightforward design, enhanced software, end-user acceptance but mostly by optimi-

sing management strategies and measures assisting local decision-making (Santos *et al*., 2013; Gillson *et al*., 2019). SD incorporates nonlinearity of complex systems using feedback loops, stocks and flows to represent key entities and process-based dynamics (Trappey *et al*., 2012). Furthermore, SD models allow expert opinion to be incorporated, projecting long-term population patterns in response to ecological constrains and environmental scenarios (Bastos *et al*., 2012; Weller *et al*., 2016; Arosa *et al*., 2017).

The Iberian-Atlantic population of Shag (*Gulosus aristotelis subsp. aristotelis)* has approximately 1,400 breeding pairs, mainly inhabiting rocky islands and islets of Galicia (Cíes Islands, NW Spain) and west Portugal (Del Moral & Oliveira, 2019). Significant declines were detected for this population (Del Moral & Oliveira, 2019), namely in Galicia (the most important Iberian population) with a reduction of 500 pairs in the last two decades (26% overall reduction) (Munilla & Barros, 2019). Nesting places are a limitation for the species and, unlike Galicia, on the Portuguese west coast there are few rocky shores, islets or islands with good conditions for breeding (Ramírez *et al*., 2008; Meirinho *et al*., 2014). In fact, most of the Portuguese relict population, circa 100 breeding pairs, inhabits the Berlengas islands and their surrounding waters (Del Moral & Oliveira, 2019; Oliveira, 2019). This population also declined in the last decades, albeit the increase in protection associated with the establishment of the Berlengas' Special Protection Area (BSPA) in 1988 (Rodrigues *et al*., 2011; Oliveira *et al*., 2016). Anthropogenic and environmental factors seem to be correlated with this population trend, such as invasion by exotic species, bycatch within different fishing gears, oil spill catastrophes, tourism disturbance, climate and oceanographic change and the increasingly common extreme weather events (Velando & Freire, 2002; Munilla *et al*., 2011). Hence, Shag might be considered, apart from a conservation perspective, an indicator of the ecological status of coastal rocky environments whose futures are interconnected (Ramírez *et al*., 2008).

Considering the multiple coexisting threats, deciding the best options for conservation may require discussing the feasibility of its implementation. Decision analysis tools, such as SD modelling frameworks, can help ranking specific management actions from the forecasted results (Santos *et al*., 2013; Arosa *et al*., 2017). Therefore, the main objective of this study was to develop a SD model to predict possible trends for the Berlengas' Shag population, considering current biological and ecological constrains, environmental conditions and their interplay with management actions. Our specific objectives were: 1) to integrate

scattered information from different studies in a SD framework, aimed at recreating realistic population dynamics; 2) to predict the outcome of competing BSPA management scenarios and determining the most effective ones; 3) to discuss the relationships between Shag population dynamics as a surrogate of the conservation status of the BSPA.

METHODS

Study area

The Berlengas Natura 2000 Special Protected Area (BSPA) (PTZPE0009, EU Birds Directive) (39° 27' 5.7" N; 9° 31' 2.2" W) comprises 102,662 ha of protected waters surrounding the Berlengas archipelago, located approximately 10 km from the Portuguese west coast (Fig. 1). The area is influenced by two geomorphological structures, the Carvoeiro Cape and the Nazaré Canyon, which intensify coastal upwelling and concomitant primary production (Fiúza, 1983). The archipelago (composed by three islands: Berlenga Grande, Estelas and Farilhões) is also an important insular ecosystem due to the occurrence of several endemic species of plants and reptiles, but also seabirds, marine invertebrates, fish and marine mammals (Mendes *et al*., 2018). In particular for seabirds, BSPA holds important breeding populations of Cory's shearwater (*Calonectris borealis*), Band-rumped storm-petrel (*Oceanodroma castro*), Yellow-legged gull (*Larus michahellis*), Lesser black-backed gull (*Larus fuscus*) and Shag (Lecoq, 2003). The area is also important to migratory species such as the Northern gannet (*Morus bassanus*) and the critically endangered Balearic shearwater (*Puffinus mauretanicus*) (Meirinho *et al*., 2014).

Conceptualisation and parameterisation of the model

The model integrates relevant information concerning Shag's biology, ecology but also environmental and anthropogenic drivers (Fig. 2) (Snow, 1960; Velando & Freire, 2002). Whenever possible, specific BSPA data was used to parametrise the model but in the absence of that, we used reference information, namely from the closest Shag colony located in the Cíes Islands (Neto, 1997; Velando *et al*., 1999; Velando & Munilla, 2008; Silva, 2015) (Table 1).

The day was selected as the appropriate time unit for simulating stochastic events (e.g. extreme weather and anthropogenic disturbance) and environmental, biological and ecological

processes affecting individuals' survival (Gonzalez *et al*., 2015). Considering the multitude and variability of processes (biological, ecological and environmental) involved, one hundred independent simulations were ran by scenario, for a period of 10 years, to gauge possible effects of management actions in the population trends (White, 2019). The initial number of adults for all simulations (adult population at t0, 1st day of January) was set as 164 (82 males and 82 females), according to the estimates from the censuses compiled in the last decade (Pereira & Oliveira, 2019) (Appendix III, 1.1 Adults). Additionally, 19 immatures and 64 juveniles were estimated also for t0, supported on average productivity and mortality rates (taking into account the previous adult population) (Velando & Freire, 2002; Velando & Munilla, 2011; Silva, 2015) (Appendix III, 1.2 Immatures and 1.3 Juveniles). Appart from the previous information, a proportion of immature individuals (47% of juvenile females) was simulated to breed in their second year of life, accordingly with Velando and Freire (2002).

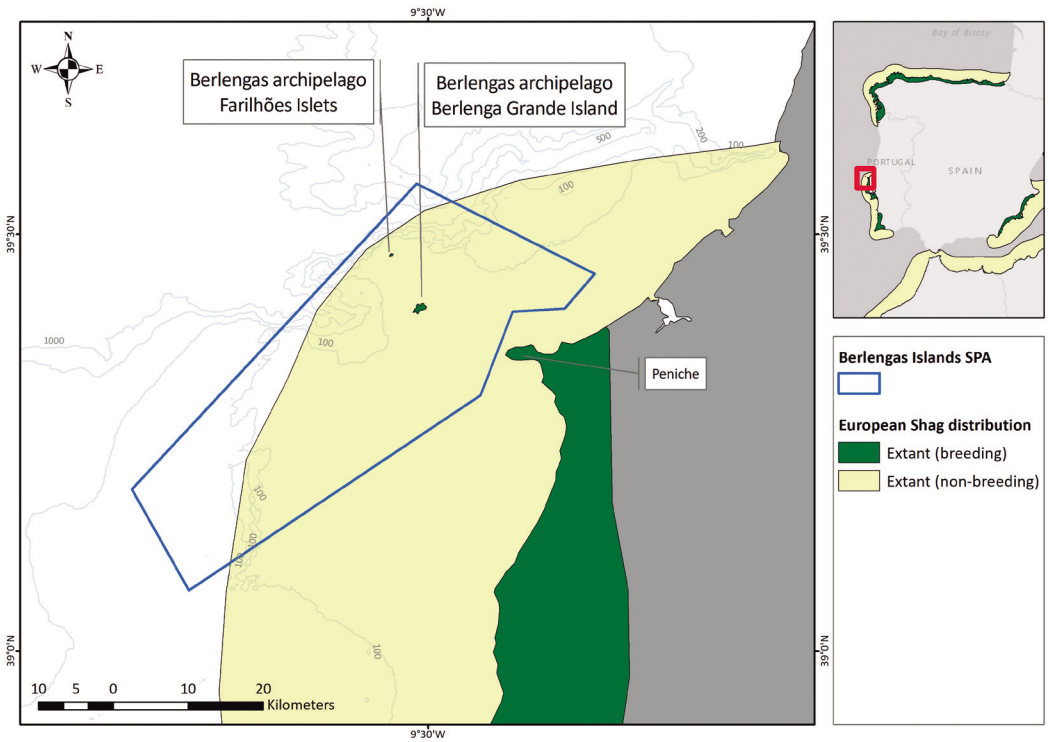


Figure 1. Map of the Berlengas Islands Special Protected Area location and the European Shag distribution (BirdLife International, 2018a).

Table 1. European Shag population dynamics in Berlengas. Specification of the main variables included in the model, respective description, units and references. Daily rates applied in the model are depicted in Appendix II and III. Additional references consulted are shown in Table S1 of Appendix IV.

Variable	Description	Unit	Source
Adults			
Initial breeding adult pairs	Max. number of breeding adult pairs male in the last decade 82	Individuals	(Pereira & Oliveira, 2019)
Productivity	Proportion of flying juveniles per nest 1.32	Rate	(Silva, Luís, & Oliveira, 2017)
Adult natural mortality rate	Proportion of dead adults per year Min 0.18 Max 0.32	Rate	(Velando & Freire, 2002)
Non-juvenile bycatch mortality rate	Proportion of dead adults from bycatch per year 0.03	Rate	(Velando & Freire, 2002)
Non-juvenile male mortality rate after spill oil catastrophe	Proportion of adult male mortality rate after spill oil catastrophe 0.00	Rate	(Velando, Munilla, & Leyenda, 2005; Martínez-Abraín *et al.*, 2006)
Non-juvenile female mortality rate after spill oil catastrophe	Proportion of adult female mortality rate after spill oil catastrophe 0.01	Rate	(Velando *et al.*, 2005; Martínez-Abraín *et al.*, 2006)
Immatures			
Initial immature population	Assumed number calculated of immature individuals 9.57	Individuals	(Velando & Freire, 2002; Silva *et al.*, 2017)
Immatures recruitment rate	Proportion of breeding in their 2 year 0.47	Rate	(Velando & Freire, 2002)
Immature mortality	Proportion of dead immature per year 0.3	Rate	(Velando & Munilla, 2008)

Table 1. (Cont,)

Variable	Description	Unit	Source
Productivity	Proportion of flying juveniles per nest Min 0.36 Max 0.77	Rate	(Velando & Freire, 2002; Velando & Munilla, 2008)
Non-juvenile bycatch mortality rate	Proportion of died immatures from bycatch per year 0.03	Rate	(Velando & Freire, 2002)
Non-juvenile male mortality rate after spill oil catastrophe	Proportion of immatures male mortality rate after spill oil catastrophe 0.00	Rate	(Velando *et al*., 2005; Martínez-Abraín *et al*., 2006)
Non-juvenile female mortality rate after spill oil catastrophe	Proportion of immatures female mortality rate after spill oil catastrophe 0.01	Rate	(Velando *et al*., 2005; Martínez-Abraín *et al*., 2006)
Juveniles			
Initial juvenile population	Assumed number calculated of juvenile individuals 31.93	Individuals	(Velando & Munilla, 2011; Silva *et al*., 2017)
Juvenile mortality	Proportion of dead juveniles per year 0.59	Rate	(Velando & Munilla, 2011)
Juvenile bycatch mortality rate	Proportion of dead juvenile from bycatch per year 0.1	Rate	(Genovart, Oro, & Tavecchia, 2017)
Juvenile male mortality rate after spill oil catastrophe	Proportion of juvenile male mortality rate after spill oil catastrophe 0.01	Rate	(Velando *et al*., 2005; Martínez-Abraín *et al*., 2006)
Juvenile female mortality rate after spill oil catastrophe	Proportion of juvenile female mortality rate after spill oil catastrophe 0.03	Rate	(Velando *et al*., 2005; Martínez-Abraín *et al*., 2006)

Table 1. (Cont,)

Variable	Description	Unit	Source
Chicks			
Chicks natural mortality rate (from adults)	Proportion of dead chicks per year 0.2	Rate	(Velando *et al*., 1999)
Chicks natural mortality rate (from immatures)	Calculated proportion of dead chicks per year 0.25	Rate	(Velando & Freire, 2002; Velando & Munilla, 2008)
Bad weather chicks mortality rate	Calculated proportion of dead chicks due to bad weather per year 0.03	Rate	(Velando *et al*., 1999)
Chicks mortality rate by rats	Proportion of dead chicks by rats per year 0.39	Rate	(Silva, 2015)
Chicks mortality rate by tourism disturbance	Proportion of dead chicks by rats per year 0.03	Rate	(Velando *et al*., 1999)
Chick mortality rate after spill oil catastrophe	Assumed to be the same than adult female mortality rate after spill oil catastrophe 0.01	Rate	(Velando *et al*., 2005; Martínez-Abraín *et al*., 2006)
Eggs			
Eggs number laid	Averaged number of eggs laid per year 2.14	Eggs	(Silva *et al*., 2017)
Egg natural failure rate (adults)	Proportion of eggs failure per year Min 0.24 Max 0.38	Rate	(Neto, 1997; Silva *et al*., 2017)
Egg natural failure rate (immatures)	Calculated proportion of eggs failure per year Min 0.48 Max 0.60	Rate	(Velando & Freire, 2002; Velando & Munilla, 2008; Silva *et al*., 2017)

Table 1. (Cont,)

Variable	Description	Unit	Source
Eggs predation rate by rats	Proportion of eggs predation rate by rats 0.64	Rate	(Silva, 2015)
Eggs mortality rate after spill oil catastrophe	Assumed to be the same than adult female mortality rate after spill oil catastrophe 0.01	Rate	(Velando *et al*., 2005; Martínez-Abraín *et al*., 2006)

Shag population dynamics and demographic parameters

Population dynamics emerges from the balance between new individuals born and natural and anthropogenic mortality influencing asymmetrically the different age-classes. In this way, the SD model is structured on five age-classes (each one associated with a state variable): egg, flightless chick, complete flying juvenile, immature (second year birds), and adult (birds aged 3 or more years old) (Fig. 2) (Appendix I, Population dynamics sub-models). A summary of the most important parameters is shown in Table 1. Complete details on the parameterization of the model based on Shag's biology and ecology are depicted in Appendix IV.

Key-factors influencing BSPA population dynamics were identified as 'Ecological', i.e. natural abiotic and biotic ones and 'Anthropogenic', for which specific management actions were tested. We have assumed anthropogenic mortality as an additive factor to base/natural mortality (Table 1).

Ecological factors

Prey availability

Shag's diet includes a diversity of fish species, captured in shallow and clear waters with good visibility (Velando & Freire, 1999). The fluctuation of the fishing stock, and particularly sandeels (family Ammodytidae), impacts the species breeding success (Furness & Tasker, 2000; Lilliendahl & Solmundsson, 2006). Actually, since the diet of chicks and juveniles is almost exclusively based on sandeels, i.e., adults can feed on a much wider spectrum of

fish, daily mortality rates due to sandeels' abundance were applied exclusively to these age classes (Howells *et al*., 2018). To increase realism, the model was designed to recreate three scenarios of sandeels' abundance (low, medium and high), which assumed a variation in the chicks and juveniles mortality rate accordingly with Cury *et al*., (2011) (see Appendix III for more details).

Adverse weather and chick mortality

Adverse weather events during May have been pointed out to upsurge chick mortality (Croxall *et al*., 2012; Newell *et al*., 2015). According to Velando *et al*., (1999), wind gusts stronger than 29 km h-1 and daytime rainfall over 10 mm reduce visibility underwater, ultimately limiting the amount of food that chicks receive from their parents. This way, the model simulates daily variations in weather conditions (in terms of rain and wind) and, faced with the impossibility of accurately predicting extreme weather events occurrences, historical trends were considered for simulating probabilities of extreme events (https://www.windguru.cz/1528, http://snirh.apambiente.pt). Whenever simulated meteorological conditions surpass the threshold defined by Velando *et al*., (1999) mortality of chicks due to adverse weather is activated (Croxall *et al*., 2012; Newell *et al*., 2015) (Table 1 and Appendix III, 2.3 Adverse weather and chick mortality).

Anthropogenic factors

Bycatch mortality

Incidental capture by different fishing gear is one of the top threats to seabirds worldwide (Dias *et al*., 2019). Shags, particularly less experienced juveniles, are captured by gillnets and longlines as proved in a short-term study in the BSPA, evidencing high bycatch rates (Genovart *et al*., 2017; Oliveira *et al*., 2018, 2020). Considering previous cited studies and complementary information, we have assumed in the model different mortality rates for non-juveniles (immature and adults) and juvenile birds associated with bycatch (García-Barcelona *et al*., 2010; Genovart *et al*., 2017; Velando & Freire, 2002) (Table 1 and Appendix III 2.1 Bycatch mortality).

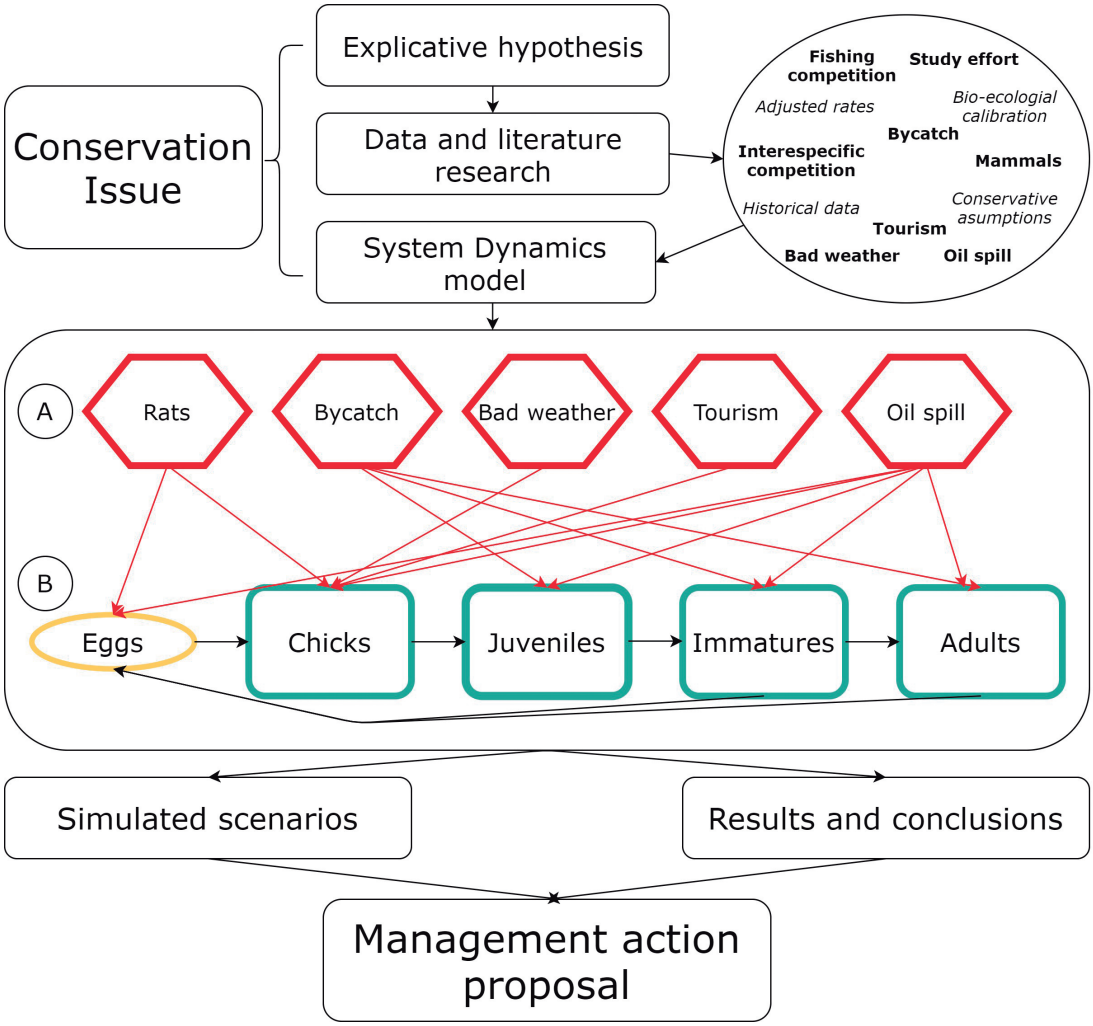


Figure 2. Dynamic model conceptual diagram. A) Main key-factors affecting the Shag population in Berlengas archipelago; B) Shag population dynamics and age-classes considered. The explanation of the connections, different age classes and key-factors can be found in Appendixes I, II and III.

Mortality due to rats

One of the most dramatic effects on the viability of seabird populations is the predation by invasive mammals such as rats and cats (Jones *et al*., 2008). The historic presence of rats in the BSPA was associated with declines of smaller seabirds and could have driven some species to extinction (Bell *et al*., 2016). Photo-trapping studies in the BSPA disclosed nest failure by rat predation and disturbance of at least 30% of Shag nests (Silva, 2015). Thus, when rats are present, the model assumes an average reduction of eggs and chicks viability accordingly with Igual *et al*., (2006) and Silva (2015) (Table 1 and Appendix III, 2.2 Mortality due to rats).

Tourism disturbance-associated mortality

Coastal tourism is growing in marine protected areas, often in core breeding and feeding grounds for seabirds, with possible effects on chick survival (Gössling *et al*., 2018; Martín *et al*., 2015; Dehnhard *et al*., 2020). During spring and summer, the shallow waters surrounding the archipelago are massively used by recreational boats, namely during weekends and holidays (Fernandes, 2016). Aggravation in chick mortality was simulated in the model during May weekends, when an overlap between recreational boats use and the presence of chicks in the nests occurs (Fernandes, 2016; Newell *et al*., 2015) (Table 1 and Appendix III, 2.4 Tourism disturbance-associated mortality).

Oil spill mortality

Oil spills have lethal effects on seabirds, often by eliminating the waterproofing of their plumage and leading to loss of insulation and buoyancy but also several physiological effects, such as pulmonary edema and endocrine disruption (Troisi *et al*., 2016). Oil spills are recurrent in the NW Iberian coast – a recent one killed 5% of the Shag population, affecting particularly females and juveniles (Velando *et al*., 2005; Martínez-Abraín *et al*., 2006). For the model, we have applied the corresponding oil spill mortality rate associated with specific mortality by sex and age (Martínez-Abraín *et al*., 2006). Based on the historical data, a random probability of a catastrophic oil spill every 9 (± 7.5) years was simulated, associated with sex and age specific mortalities (ITOPF, 2007). This mortality rates were applied during one year after an oil spill occurrence, in compliance with Martínez-Abraín *et al*., (2006) (Table 1 and Appendix III, 2.5 Oil spill mortality).

Sensitivity analyses

In order to provide a measure of the robustness of the model, a Sensitivity Analysis (SA) was performed, testing the sensitivity of the obtained results to changes in the parameters, forcing functions and/or sub-models (Lee *et al*., 2015). This SA was done by one-parameter-at-a-time technique (OAT), changing the population parameters of the model with +/– 10% and +/– 50% variation of the respective values and observing changes in the response of the most important state variables, adults, immatures, juveniles, chicks and eggs (Ligmann-Zielinska, 2013).

Scenarios

To predict future trends for the BSPA population and envisage the most effective conservation strategies, our model incorporates the key factors specified previously with comprehensive management actions. Explicitly, the management actions associated with each scenario reduce or remove one or more of the 'Anthropogenic factors' while considering pertinent 'Ecological factors' dynamics. The number of adult females (the most critical sex-age class for sustaining a population in a monogamous species such as Shag) was defined as the core variable for gauging population dynamics and, subsequently, comparing the management actions (and scenarios) implemented (Spelt & Pichegru, 2017). Eight scenarios were projected, considering sundry likelihoods and resources available for conservation (Table 2).

In scenario 1, our baseline scenario, no management actions were implemented and, in this way, all factors were considered in the simulation. The results are expected to reflect the population trend in recent years and were used to assess the effectiveness of the actions implemented in the other scenarios.

Scenario 2 simulates the removal of bycatch-associated mortality by implementing an exclusion of fisheries in the BSPA waters. Although, for socio-economic reasons this is most unlikely, the outcomes could provide pertinent information to outline regulations for specific areas and/or periods.

Scenario 3 simulates the elimination of rats in the archipelago, carried out in the BSPA in 2016 (Oliveira *et al*., 2017). This scenario is especially interesting to be compared, apart from the baseline scenario, with real data associated with the monitoring programs and future reports.

In scenario 4, disturbance from tourism was disregarded, namely during May weekends, when boats displace adults from the most productive feeding areas and chicks are still highly dependent. If effective in terms of conservation, this scenario could be possibly implemented by restricting access to the shallow waters of the BSPA.

Scenarios 5-6-7 combine the previous ones, namely 2 and 3 (scenario 5), 3 and 4 (scenario 6) and 2 and 4 (scenario 7). This was considered important to discuss, regarding logistics and budget, effort-effectiveness of adding more than one management action.

Finally, scenario 8 contemplates the unlikely situation in which all 'Anthropogenic factors' have been removed (apart from oil spills, considered impossible to prevent and to solve using local management actions), mostly improbable but fundamental to gauge the overall anthropogenic stress when comparing with the other scenarios (especially scenario 1) (Table 2).

We used STELLA software (version 9.0.3; Isee Systems, Inc.) to conceptualise the dynamic model. This software is a popular system dynamic modelling platform, integrating conceptual diagrams with mathematical equations (Naimi & Voinov, 2012). All processes explanation, flow diagrams and equations are depicted in the appendices I, II and III. More detailed information and supplementary bibliography consulted are depicted in Appendix IV.

Statistical analysis

Cohen's effect size was computed to reveal the magnitude of the differences in the projected population of adult females (after 10 years) between scenarios (Cohen, 1988; Santos *et al*., 2016b). Cohen's d estimate can be interpreted as negligible (d<0.2), small (d=0.2-0.49), medium (d=0.5-0.79) or large (d>0.8) (Lakens, 2013). To complement effect sizes, a Generalized Linear Model (GLzM), using adult females as response variable was applied (Donald, 2007). The model was fitted with a Quasi-Poisson distribution, in order to compensate the over-dispersion of data (mean 86.29; variance 365.94) (Crawley, 1993). Finally, to analyse the differences between paired scenarios, the Steel-Dwass posthoc test, especially useful for discriminating all-pairs comparisons (Morley, 1982), was applied (also for juvenile females, considering that half are breeders, see please Appendix IV). All statistical analyses were carried out using 'PMCMRplus' (Pohlert, 2020), 'Steel.Dwass.test' (Douglas Steel *et al*., 2017), 'effsize' (Torchiano, 2020) and 'stats' package on the software R (R Development Core Team, 2020).

Table 2. Scenarios simulated for the Berlengas Shag population throughout the 10 years of simulation. Manipulated key variables, accordingly with the scenario - Anthropogenic factors: bycatch, rats, disturbances and oil spill. Non-manipulated variables - Ecological factors: prey availability and bad weather. * Although the oil spill is an Anthropogenic factor, it was not considered manageable through local actions, but mostly a stochastic factor.

Scenario	Key Variables	Pressures
1	baseline scenario	Anthropogenic factors (bycatch + rats + disturbances + oil spill*) + Ecological factors
2	no bycatch	Anthropogenic factors (rats + disturbances + oil spill*) + Ecological factors
3	no rats *(scenario after 2016)*	Anthropogenic factors (bycatch + disturbances + oil spill*) + Ecological factors
4	no disturbance	Anthropogenic factors (bycatch + rats + oil spill*) + Ecological factors
5	no rats no bycatch	Anthropogenic factors (disturbances + oil spill*) + Ecological factors
6	no rats no disturbance	Anthropogenic factors (bycatch + oil spill*) + Ecological factors
7	no bycatch no disturbance	Anthropogenic factors (rats + oil spill*) + Ecological factors
8	no rats no bycatch no disturbance	Anthropogenic factors (oil spill*) + Ecological factors

RESULTS

Sensitivity analysis

The results from the OAT sensitivity analysis highlights the state variables adults, immatures, juveniles (females and males), chicks form adults and chicks from immatures, as the most responsive to manipulation of parameters (Table S6 in Appendix V). Specifically, small changes in the parameters number of laid eggs, bad weather chicks' mortality and non-juvenile bycatch mortality rate had critical influence in the outcomes of model, namely by affecting most of the state variables' results (Table S6 in Appendix V).

Scenarios' outcomes for the next decade

Our baseline scenario (scenario 1) resulted in a predicted reduction of 7.90% in the adult females (hereon population) (min: -13.60%; max: -2.13%) (Fig. 3, 3.1), most likely compromising its med/long-term viability, while a population increase of 13.52% (min: 5.02%; max: 22.12%) was estimated if fishing was forbidden in the BSPA, by eliminating bycatch (scenario 2) (Fig. 3, 3.2).

On the other hand, the eradication of rats (scenario 3), increased the population in 48.50% (min: 34.61%; max: 62.49%) (Fig. 3, 3.3), whereas forbidding recreational boats during the weekends of May (scenario 4) was associated with a population decrease of 5.27% (min: -13.89%; max: 3.50%) (Fig. 3, 3.4).

When rats' eradication was combined with no fishing (scenario 5), the results depicted an increase of 83.61% (min: 67.32%; max: 100.07%) (Fig. 3, 3.5). Conversely, rats' eradication combined with no tourism (scenario 6) is expected to produce an increase in the population of 50.39% (min: 37.10%; max: 63.81%) (Fig. 3, 3.6) while no fishing and no tourism (scenario 7) could yield a population increase of 13.04% (min: 5.23%; max: 20.93%) (Fig. 3, 3.7).

Finally, for scenario 8, where all 'Anthropogenic factors' were simulated to be removed (apart from oil spills), increases in the population of approximately of 86.21% were forecasted (min: 67.69%; max: 104.94%) (Fig. 3, 3.8).

Large changes in the population were predicted when comparing the baseline scenario with all others, except for scenario 4 (no disturbances), which only shows a small difference (Cohen's effect size, Table 3). Especially large differences were expected for scenarios 5

and 8 (no rats and no bycatch; no rats, no bycatch and no disturbance) (Table 3). As expected from the previous results, the most significant (associated with higher t-values) were simulated for scenarios 5 and 8 (Table S4 in Appendix V). Additionally, the pairwise comparisons between all scenarios for adult females and juvenile females were found to be statistically significant different (Adult female, chi-squared = 4636.8, df = 7, p-value < 0.001; Juvenile female, chi-squared = 5041.3, df = 7, p-value < 0.001), except between scenarios 2-7, 3-6 and 5-8 (Table S5 in Appendix V and Fig. 4).

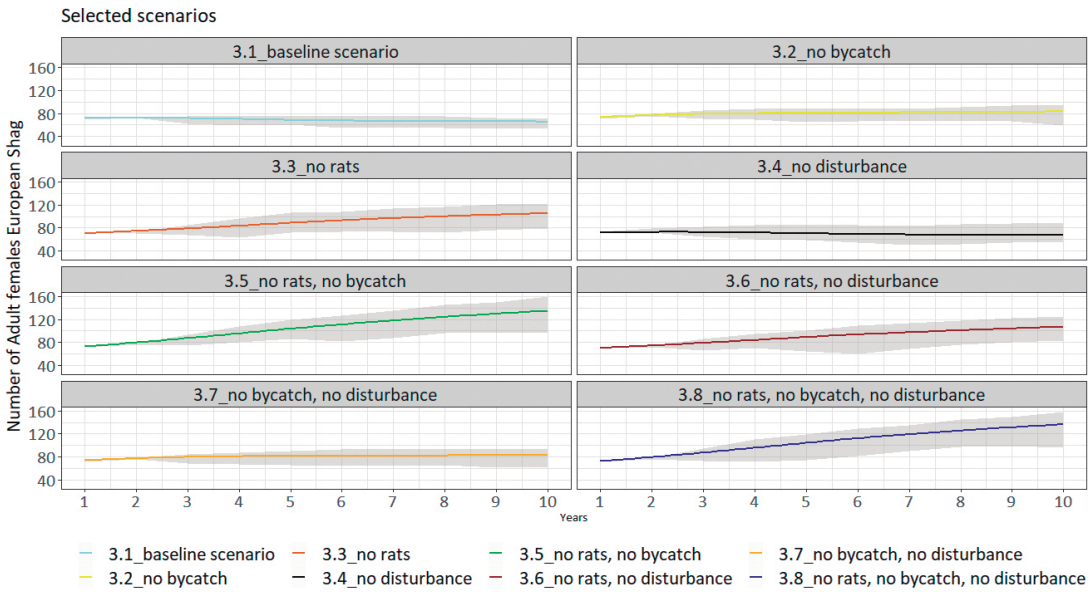


Figure 3. Adult females' average trend by scenario. A period of 10 years, using 100 independent simulations, was considered by scenario. Grey shade shows maximum and minimum simulation values reached by scenario.

Table 3. Comparison of the results obtained between the baseline scenario (scenario 1) and all other scenarios using effect sizes. Cohen's d estimate, effect sizes using Cohen estimator; lower and upper 95% CI represents 95 percent confidence interval, and Interpretation shows the magnitude of Shag population change between scenarios. 1: baseline scenario (scenario 1); scenario 2: no bycatch; scenario 3: no rats; scenario 4: no tourist disturbances; scenario 5: no rats, no bycatch; scenario 6: no rats, no tourist disturbances; scenario 7: no bycatch, no tourist disturbances and scenario 8: no rats, no accidental capture, no tourist disturbance. Complementary comparisons are depicted in Table S3 Appendix V.

Pairwise comparisons	Cohen's d estimate	lower 95% CI	upper 95% CI	**Interpretation**
1:02	3.63	4.09	3.18	**large**
1:03	5.54	6.16	4.93	**large**
1:04	0.42	0.70	0.14	**small**
1:05	8.16	9.01	7.31	**large**
1:06	6.03	6.69	5.37	**large**
1:07	3.75	4.22	3.29	**large**
1:08	7.49	8.28	6.7	**large**

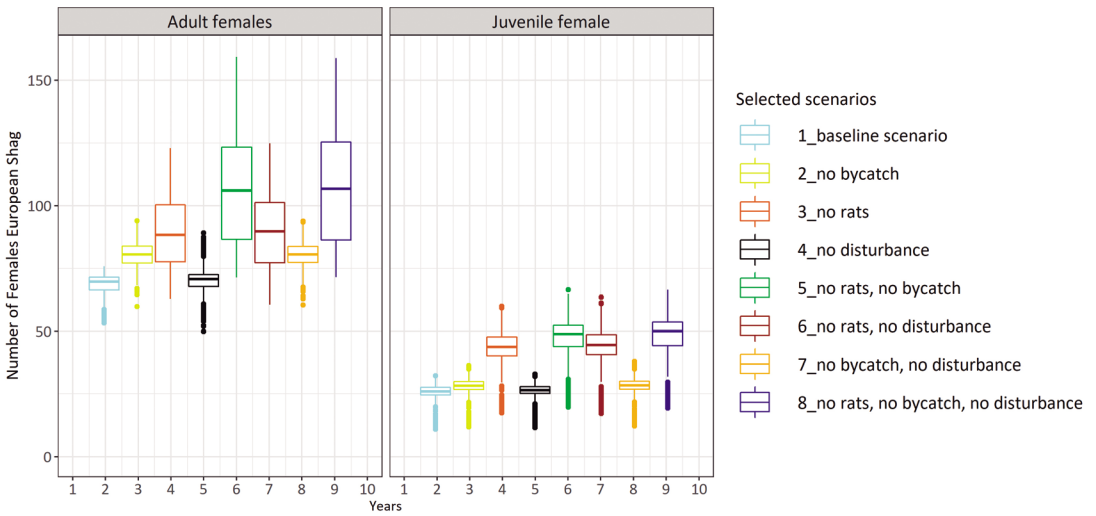


Figure 4. Boxplots comparing adult and juvenile females' average trend for all scenarios. A period of 10 years, using 100 independent simulations, was considered by scenario. The lower and upper limits of each box represent the first and third quartiles, respectively, and the line inside each box represents the median. The bottom and top bars represent the minimum and, respectively. Circles outside the first and third quartiles range are outliers.

DISCUSSION

Simulated population trends and effectiveness of management actions

Our baseline scenario estimates a decrease of 7% for the adult females, in line with the trends detected for the BSPA population in recent years (Oliveira, 2019; Pereira & Oliveira, 2019). Anyway, a large inter-annual variation in the number of breeding pairs characterises this population (e.g., ~35 pairs in 1978, ~90 pairs in 1995, ~15 pairs 1998, ~80 pairs in 2002, ~32 pairs 2008, ~ 82 pairs in 2012, ~38 pairs 2014 and 62 pairs in 2019). This variation might be associated with different census methods, difficulties in monitoring inaccessible nest locations but mainly due to the number of females that do not reproduce yearly due to poor physical condition (Neto, 1997; Oliveira, 2019; Pereira & Oliveira, 2019).

Our results highlight the proficiency of rats' eradication and fisheries control, by removing bycatch, for Shag conservation (Table 3 and Table S4 in Appendix V) (Jouventin *et al*., 2003; Bell *et al*., 2016; Avery *et al*., 2017). In fact, rats (*Rattus spp.*) are present in most of the world's major islands and are known to negatively affect island biota, exacerbated by endemic or small population sizes that are inherently susceptible to extinction (Atkinson, 1996; Oliveira *et al*., 2017). Recent efforts to eradicate rats from the archipelago should show its results in the next years (Oliveira *et al*., 2017) as many successful examples pinpoint the effects of rats' removal from islands on seabird conservation (Russell & Holmes, 2015; Jones *et al*., 2016). Actually, the maintenance of a rat-free archipelago could result, according to our simulations, in more than 100 additional breeding pairs for the next decade.

On the other hand, removing bycatch mortality is highly unlikely to be implemented, due to the importance of the BSPA for fisheries and local socio-economy (Melvin *et al*., 1999). We have used conservative rates associated with this factor but we must not forget that exceptionally massive mortality events can occur and these random events can be extremely important and even cause extinction in small populations (Boyce, 1992). Different mitigation measures (visual, acoustic signals, setting time, setting depth) have been tested, although with inconclusive results for Shag (Martin & Crawford, 2015; Oliveira *et al*., 2020). Therefore, to minimize bycatch in different fishing gear, halting fisheries in shallow areas and reducing fishing pressure could be considered effective measures, that ultimately could also contribute to increase fish stocks and the conservation of other species (e.g. seabirds, sea mammals) (Melvin *et al*., 1999), such as the critically endangered Balearic shearwater or Northern gannet (Oliveira *et al*., 2020).

Disturbance caused by tourism and oil spills had minor effects on the population trends, probably because visits occur mostly in July and August when chicks are no longer in the nest (Silva, 2015; Fernandes, 2016) and the low probability of oil spills considered for the simulated period. However, tourism in natural areas continues to increase with unflattering consequences (Marcella *et al*., 2017), and only an oil spill event might have dramatic consequences for this relict population (Velando *et al*., 2005; Munilla *et al*., 2011).

Environmental and oceanographic change

Our model does not explicitly evaluates the impacts of global climate and oceanographic change in the population dynamics, because the inter-annual variation in conditions predicted for the next decade should be higher than the expected trend (IPPC, 2018). However, we have consider factors emerging from that variation, such as the mortality of chicks associated with adverse weather conditions and juvenile and chick mortality rates related with prey abundance (Velando *et al*., 1999; Furness & Tasker, 2000). In fact, chick mortality due to extreme meteorological events was considered a determinant parameter in the sensitivity analysis (Appendix IV, Table S6). Despite the fact that a 10 years' period only allows very incipient conclusions to be drawn, the prediction of more extreme climate events in the future, namely increasing days with heavy rains and strong winds and a decrease in the main food source, might have detrimental effects on chicks' survival (Grémillet & Boulinier, 2009). Even though seabird declines are highly correlated with sea temperatures rising, we consider fundamental more investigation on this scope, to increase our knowledge on the interplay between climate/ocean trends and trophic networks (Jenouvrier *et al*., 2018).

Evaluation of model assumptions and potential biases

When compared to other modelling methodologies, such as the widely used Species Distribution Models (SDM), System Dynamics frameworks are considered more flexible, transparent and useful to understand and simulate processes at local scales (Santos *et al*., 2015). This said, evaluation of assumptions made during the conceptualisation of demographic models is of utmost importance (Sydeman *et al*., 2017; Sæther & Engen, 2019). In fact, even if the trends depicted seem consistent, some parameters and state variables, such as the inherently imprecise initial population size (Neto, 1997; Pereira & Oliveira, 2019) or

the mortality rate due to stochastic events, could have influenced the obtained results. To minimize these drawbacks, instead of using specific values that could steer the results, we have used distributed values accordingly with specific ranges, estimated from minimum and maximum values (from literature) and conservative probabilities of phenomena occurrences. Another potential weakness in demographic models may be the assumption of anthropogenic mortality as additive to natural mortality (Péron, 2013). Clearly separating natural from anthropogenic mortality is itself dubious and some authors assume general rates for both types (Aanes *et al*., 2007).

Complementary ideas and uncertainties

Cost-effective monitoring and management of conservation areas are regularly achieved using umbrella and/or indicator species (Simberloff, 1998; Hawkes *et al*., 2019). As a marine top predator, Shag could play a relevant role by indicating the ecological status of rocky shore marine areas such as the BSPA (Hunter *et al*., 2016). In fact, the species is sensitive to a wide range of socio-ecological factors such as invasive mammals, human disturbance, fisheries competition and overlapping with feeding areas, as well as climate/oceanographic changes. In this way, the species is capable of capturing the complexities of the ecosystem, while remaining simple enough to be easily monitored by standard methodologies (Siddig *et al*., 2016).

On the other hand, dynamic models such as the one developed in our study could help implementing European directives of the Natura 2000 Network (Directive 1992/43 EC; Directive 2009/147/EC) to marine SPAs, by selecting cost-effective management policies for habitats and species. This type of frameworks could help envisioning the ecological consequences of conservation actions and, even though our results are linked with a specific area of the Iberian-Atlantic arc and seabird species, the methodology presented could be easily parametrised to other areas, species and problematics (Bastos *et al*., 2012; Arosa *et al*., 2017; Petrescu Bakış *et al*., 2021).

We have described and analysed the probable impacts of ongoing disturbances on the viability of a small relict population (Highlights in Appendix VI). However, effective conservation should move forward relentlessly trying to anticipate new threats or investigate those we do not yet know about. Recent studies show new stress factors, particularly micro-

plastics, found in more than 60% of Shag pellets and whose effects are mostly unknown (Álvarez *et al*., 2018). Also, projected off-shore windfarms for this coast, which are particularly attractive to Shags (but also to other seabirds) could produce an additional source of mortality (Dierschke *et al*., 2016). To finish, we cannot forget the isolated situation of the small population of Shag in BSPA, susceptible to genetic drift and inbreeding depression (Velando *et al*., 2015).

Based on the results obtained, we suggest investigating the following management recommendations: 1) interrelate, using monitored data, the breeding population of Shag, meteorological/oceanographic conditions and fish populations in the BSPA; 2) monitor invasive mammals in BSPA and respond rapidly with pertinent actions if a re-invasion occurs; 3) apply mitigation measures in fishing gear and consider closing to fisheries specific Shag foraging areas during the breeding season; 4) reduce the number of tourists visiting BSPA, especially during the breeding season. These ideas, if applied, might contribute to increase our knowledge and conservation of Shags and the ecological status of the BSPA.

CONCLUSIONS

The ability to accurately predict species responses to environmental change is crucial for conservation planning and to support key ecosystem management actions (Kandziora *et al*., 2013). Despite all the assumptions and weaknesses that this academic work may present, the dynamic model developed integrates disperse information concerning the biology and ecology of Shag, estimating the likely outcome of different conservation actions directed to a relict population. The results obtained stress the importance of controlling invasive mammals and bycatch to conserve and recover Shag populations and concomitant coastal ecosystems (Bull, 2007; Oliveira *et al*., 2017) (Fig. S1 in Appendix VI).

DISCUSIÓN GENERAL

El conocimiento de la demografía de los seres vivos nos permite conocer cómo funcionan sus poblaciones, cómo interactúan con su entorno cambiante y cómo se adaptan a esos cambios (Thomson *et al*., 2008). En este sentido, el estudio de la distribución de los organismos y su dinámica poblacional constituyen dos de los temas centrales de la ecología (Lebreton & Clobert, 1991; Morris, 2003; Elith *et al*., 2006; Newman *et al*., 2014; Chudzińska *et al*., 2015).

Diversas teorías clásicas analizan la distribución de animales que compiten por recursos que se distribuyen de manera no uniforme o en parches, como ocurre en el medio oceánico. La teoría de la distribución ideal libre (IFD) (Fretwell & Lucas, 1970) predice que, bajo determinadas condiciones y supuestos (todos los individuos tienen el mismo acceso al recurso, pueden moverse libremente entre parches de recursos y tienen información perfecta sobre la calidad y cantidad de recursos y competidores), la distribución de los organismos se concentrará en aquellos parches donde el beneficio sea mayor. Por lo tanto, sería esperable que los organismos se encontraran allí donde se encuentre y sea más abundante su recurso. Sin embargo, las asunciones limitantes de esta teoría, que difícilmente se cumplen en el medio natural (Křivan *et al*., 2008), hacen que rara vez los depredadores apicales –como aves o mamíferos– se ajusten a una IFD. Diversos factores, como las interacciones sociales (Bock & Jones, 2004; McLoughlin *et al*., 2006; Boyce *et al*., 2016) o la relación entre la productividad ambiental y la riqueza de especies, complican la selección del hábitat de estos organismos (Křivan *et al*., 2008).

En el caso de los depredadores marinos apicales se puede asumir que el principal recurso, fuera de la época de cría, es la búsqueda de alimento. De esta manera, cabe esperar que exista un elevado solapamiento entre las distribuciones de dichos depredadores y de las presas que consume (Sih, 1984; Mehlum *et al*., 1996; Sveegaard *et al*., 2012). No obstante, estudios más recientes han demostrado que estas relaciones son más complejas y pueden estar condicionadas por diversos factores que no son tan evidentes (Boyd *et al*., 2015; Carroll *et al*., 2017; Astarloa *et al*., 2019) y, por lo tanto, la búsqueda de estos factores subyacentes es primordial.

En los ecosistemas marinos pelágicos, el análisis de las relaciones depredador-presa resulta particularmente complejo por las siguientes razones:

1. El ecosistema pelágico es particularmente dinámico y su estructura está determinada por procesos que interactúan a diversas escalas espaciales y temporales, lo que dificulta su análisis (Caballero *et al*., 2014).
2. Los depredadores marinos tienen una alta capacidad de movimiento, pudiendo realizar grandes desplazamientos entre distintas áreas oceánicas en diferentes momentos para la búsqueda de alimentos (Scales *et al*., 2014).
3. La escasez de datos espaciales de ecosistemas marinos (Townsend *et al*., 2014) y las costosas campañas (económica y logísticamente) dificulta la investigación científica en áreas marinas (Pettex *et al*., 2017).

Ante esta situación, el desarrollo en las últimas décadas de los métodos de teledetección ha permitido incrementar de forma exponencial la información de la que disponemos de los ecosistemas marinos, proporcionando un gran número de parámetros sobre el estado y la evolución de los océanos y mares. La integración de estos parámetros a través de modelos probabilísticos ha permitido explicar y predecir los cambios en la distribución y los movimientos de un gran número de elementos de la biodiversidad marina.

Además, la creciente diversidad en el tipo de modelos aplicables y la potencia computacional de la que se dispone actualmente proporcionan todo un abanico de posibilidades para tratar de comprender de manera simplificada el ecosistema marino. De entre los modelos más usados recientemente en el estudio del ecosistema marino, podemos encontrar sencillos modelos para detectar patrones espaciales analizando la densidad de la ocurrencia de una determinada especie, como por ejemplo los análisis de densidad Kernel (Fieberg, 2007), modelos mecanicistas donde se simulan posibles escenarios futuros del ecosistema basados en la representación de los procesos ecológicos relevantes para el problema a abordar (Blanco, 2013), hasta modelos correlativos, donde se estudia el hábitat o nicho ecológico mediante el análisis de las relaciones entre la ocurrencia de la especie a estudiar y las variables de interés (p. ej., variables ambientales, climatológicas, espaciales, temporales, ocurrencia de otras especies, etc.) (Melo-Merino *et al*., 2020). Sin embargo, no debemos olvidar que los modelos no dejan de ser aproximaciones de la realidad, simplificaciones de las relaciones que observamos en el medio y que, por tanto, asumirán una parte imposible de explicar o predecir del fenómeno que se modele. Ante esta cuestión, el modelador debe obtener el modelo más simple posible que explique la realidad que observa sin olvidar que el modelo debe ser

tan complejo como sea necesario para explicar dicha realidad. Por ello, ante las diferentes ventajas e inconvenientes que presentan las diferentes técnicas de modelado aplicables a la ecología del medio marino, muchos autores proponen aplicar diferentes aproximaciones o conjuntos de modelos a la hora de obtener conclusiones más coherentes y robustas (Araujo & New, 2007; Oppel *et al*., 2012).

En el medio oceánico, generalmente oligotrófico, distintos trabajos han identificado las áreas con elevada productividad primaria como puntos calientes o *hotspots* de biodiversidad. Estas zonas atraen a un elevado número de organismos y, entre ellos, a muchos depredadores marinos (Hazen *et al*., 2013). De esta forma, se han utilizado indicadores de esa productividad –principalmente, la clorofila o la presencia de afloramientos y frentes oceánicos– para explicar la presencia y la distribución de depredadores marinos, obteniendo altas correlaciones (Louzao *et al*., 2012; Cotté *et al*., 2015). No obstante, el medio marino es un sistema particularmente dinámico, en el que las interacciones entre los factores abióticos (p. ej., vientos, corrientes, movimientos de masas de agua, etc.) y bióticos se producen a diferentes escalas espaciales y temporales (Vargas *et al*., 2003). Esto hace que procesos concatenados (p. ej., la entrada de materia orgánica en el sistema y la aparición de *bloom* de fitoplancton) no siempre ocurran en el mismo espacio y el mismo tiempo (Renault *et al*., 2016). La traslación de estos procesos a través de las redes tróficas en sistemas con alto dinamismo conlleva desacoplamientos espacio-temporales que pueden dificultar la identificación de las relaciones entre la presencia de depredadores apicales e indicadores de la productividad biológica. De esta forma, si asumimos el principio de que sólo las zonas con alta productividad primaria corresponden con las áreas clave para la biodiversidad, podríamos estar dejando fuera otras áreas importantes utilizadas por los depredadores y sus presas.

Además de identificar las áreas clave donde se distribuyen los organismos y los factores que determinan en mayor o menor medida su ocurrencia en dichas áreas, el conocimiento de la dinámica poblacional de especies amenazadas es una herramienta fundamental para anticiparnos a los problemas de conservación que afectan a dichas especies (Lebreton & Clobert, 1991). Una de las metodologías más utilizadas para abordar esta problemática han sido los Análisis de Viabilidad Poblacional (Population Viability Analysis, PVA). Estos análisis tratan de estimar el crecimiento –o decrecimiento– poblacional, ya sea bajo las condiciones actuales o las esperadas tras aplicar medidas de gestión (Boyce, 1992). De esta manera,

pueden obtenerse modelos que describen el riesgo de extinción de especies amenazadas si no se llevan a cabo medidas oportunas que aseguren su conservación (Genovart *et al*., 2016; Benson *et al*., 2019). No obstante, muchos autores encuentran limitaciones en estos PVA, como son la sobreestimación del riesgo de extinción o la simplificación en las interacciones de las especies con el medio y sus potenciales efectos (Brook *et al*., 2000; Reed *et al*., 2002; Sabo & Gerber, 2007; Lucas, 2020). Ante esta situación, modelos desarrollados a medida para propósitos concretos, como es el caso de los modelos de dinámica de sistemas, pueden ofrecer resultados más precisos (Bennett *et al*., 2019). Estos modelos dinámicos son cada vez más utilizados y se han convertido en una herramienta fundamental en ecología, ya que fusionan información dispersa de la biología de la especie y las amenazas que sufre dentro de un marco común, además de predecir las consecuencias futuras de escenarios alternativos de manejo (Warwick-Evans *et al*., 2016; Weller *et al*., 2016).

Una vez identificados los factores que amenazan la viabilidad de una especie, es fundamental decidir y priorizar las mejores medidas de gestión a aplicar para garantizar su conservación. En este sentido, los modelos dinámicos ayudan claramente al gestor a clasificar las acciones de gestión específicas a partir de los resultados predichos por los modelos (Santos *et al*., 2013; Arosa *et al*., 2017).

En este contexto, los trabajos presentados en esta tesis doctoral utilizan distintos modelos espaciales y poblacionales para el análisis de la distribución y la dinámica poblacional de las aves marinas protegidas en la península ibérica. Así, a partir del desarrollo de distintas técnicas, se aporta información sobre la distribución de las aves marinas en el Golfo de Cádiz y los factores que la condicionan, esencial para la conservación de sus poblaciones. De la misma manera, se utilizan modelos demográficos para evaluar los riesgos a los que se enfrentan poblaciones sensibles de aves marinas en el archipiélago de las Islas Berlengas, prediciendo su dinámica poblacional ante diferentes estrategias de manejo.

Gracias a los resultados obtenidos, ofrecemos herramientas para mejorar el estado de conservación de especies indicadoras del medio marino y evaluamos la eficacia de las áreas marinas protegidas, a la vez que identificamos las variables, relaciones y procesos que determinan la ocurrencia y viabilidad de dichas especies en el área de estudio.

Por último, ponemos de manifiesto la necesidad de implementar planes de gestión reales y eficaces en las áreas marinas protegidas. Estos planes deben incorporar información

de calidad desde un punto de vista ecosistémico, en el que se consideren especialmente las relaciones tróficas depredador-presa, al igual que los impactos antropogénicos que amenazan la supervivencia de estas especies centinelas del medio marino.

El seguimiento a largo plazo mejora la delimitación de las áreas marinas protegidas

Los resultados obtenidos en el primer capítulo de esta tesis doctoral nos han permitido establecer las áreas clave para la pardela balear en un período crucial de su ciclo de vida, como es la migración post-reproductora. Durante este período, la práctica totalidad de la población mundial de esta especie, críticamente amenazada, abandona el Mediterráneo para buscar áreas de alimentación a lo largo del Atlántico Nororiental (Guilford *et al*., 2012). Nuestros datos demuestran que una porción importante de esta población (que puede superar el 50% en algunos años) utiliza de manera regular el área marina ubicada entre la desembocadura del Guadalquivir y la Bahía de Cádiz para alimentarse en este período. La disponibilidad de un conjunto de datos recogidos a lo largo de nueve años de campañas permite demostrar la consistencia espacial y temporal en el uso de esta zona por parte de la especie, lo que incrementa su importancia como área clave para su conservación (Tancell *et al*., 2013; Robertson *et al*., 2014a; Meier *et al*., 2015).

En 2014 se declara por parte del Estado Español la ZEPA Área Marina del Golfo de Cádiz (BOE, 2014), que abarca 2.314,20 km^2 siguiendo la propuesta de IBA elaborada por SEO/BirdLife (Arcos *et al*., 2009). Esta declaración debería suponer una protección efectiva de las áreas clave para las aves marinas en esta zona, pero, ¿coinciden los límites de esta área marina protegida con las áreas clave de una de las especies que requiere mayor protección? Ante esta pregunta, nuestro trabajo muestra la limitada eficacia de la ZEPA del Golfo de Cádiz para la protección de una de las principales especies para la que fue declarada, la pardela balear. Tras identificar el área clave para la especie en el área de estudio, nuestros resultados demuestran que la delimitación actual de la ZEPA cubre menos del 40% de dicha área clave y, por lo tanto, esta área marina debería ser ampliada para cubrir la totalidad del área identificada.

Esta deficiencia encontrada en nuestro área de estudio no parece un caso aislado y diversos trabajos apuntan a que otras muchas áreas marinas protegidas no solapan con las distribuciones de depredadores marinos que tratan de proteger, en particular con aquellas

especies de carácter pelágico (Game *et al*., 2009; Briscoe *et al*., 2016; Critchley *et al*., 2018). La delimitación perfecta y exacta de un área marina protegida es objetivo difícilmente alcanzable, puesto que la gran movilidad de la mayoría de las especies pelágicas y la complejidad del medio marino obligaría a proteger zonas excesivamente grandes para poder reducir eficazmente los impactos antropogénicos (Pendleton *et al*., 2018). El esfuerzo y los elevados costes –directos e indirectos– de crear y mantener estas áreas protegidas tan grandes nos lleva a la situación actual, donde los recursos se dirigen a declarar y gestionar zonas más reducidas y localizadas (Kaplan *et al*., 2010). Esta situación nos obliga a ser especialmente rigurosos a la hora de establecer los límites de un área protegida. Sin embargo, la realidad es otra y diversos estudios que han llevado a la definición de AMP muestran limitaciones de tiempo y recursos para obtener información básica, lo cual pone de manifiesto que series largas temporales con datos de calidad son indispensables (Briscoe *et al*., 2016; García-Barón *et al*., 2020).

Los resultados obtenidos tras el seguimiento de las aves marinas en el Golfo de Cádiz en un período prolongado de nueve años nos han proporcionado unos datos de enorme calidad y que son realmente útiles para mejorar los límites de la ZEPA del Golfo de Cádiz. En este sentido, se ha realizado una propuesta al Ministerio para la Transición Ecológica y el Reto Demográfico del Gobierno de España para la ampliación de esta ZEPA, que abarque el área delimitada en nuestro trabajo. La propuesta ha sido aceptada y será próximamente implementada en el marco del proyecto LIFE IP INTEMARES (LIFE15 IPE/ES/000012).

¿Qué factores determinan la distribución de las aves marinas en el Golfo de Cádiz?

Una vez identificada el área clave para la pardela balear, el siguiente paso en la investigación llevada a cabo en esta tesis doctoral fue preguntarnos cuáles eran los factores que determinaban la ocurrencia habitual de esta y otras especies de aves marinas en el área de estudio. Trabajos previos han identificado diversos predictores de la presencia de las especies objeto de estudio en distintas áreas marinas. En estos estudios, factores como la concentración de clorofila, la temperatura superficial del agua, la profundidad o la presencia de frentes oceánicos, determinan de manera general los patrones de distribución de las aves marinas (Louzao *et al*., 2006a; Araújo *et al*., 2017; Serratosa *et al*., 2020).

En base a esta información previa, en un primer paso, se emplearon diferentes técnicas de modelado (MaxEnt y modelos lineales generalizados mixtos) para testar las relaciones entre la distribución de la pardela balear con los factores oceanográficos estáticos y dinámicos del área de estudio, utilizando un amplio set de datos durante el período no reproductor de la pardela balear. La utilización de diferentes aproximaciones metodológicas permite solventar las posibles limitaciones de cada método de modelado y aumentar la robustez de las predicciones (Oppel *et al*., 2012). Los resultados de los modelos ensayados coincidieron en señalar inicialmente a factores abióticos, como la batimetría, como predictor principal en la ocurrencia de la pardela balear en el área de estudio. Estos resultados difieren con buena parte de los estudios llevados a cabo para esta especie, que muestran como predictor principal de su distribución a indicadores de la producción primaria como la concentración de clorofila (Grémillet *et al*., 2008; Louzao *et al*., 2012; Araújo *et al*., 2017; Martín *et al*., 2020). Nuestros resultados muestran que la especie se concentra en áreas poco profundas de la plataforma continental y particularmente cerca de la desembocadura del río Guadalquivir. La falta de correlación espacial entre la ocurrencia de la especie y las zonas con mayores concentraciones de clorofila puede estar motivada por el alto dinamismo de la zona, con sus fuertes regímenes de viento y deriva litoral (Prieto *et al*., 2009) que propician un desacoplamiento espacio-temporal entre la aparición del fitoplancton (clorofila) y el desarrollo del zooplancton y los pequeños peces pelágicos sobre los que se alimenta la especie.

Entendiendo que el principal recurso para un depredador marino fuera de la época de cría está relacionado con la disponibilidad del alimento, cabe esperar que exista una relación entre la distribución de estos depredadores y de las presas sobre las que se alimenta (Fretwell & Lucas, 1969; Davoren, 2013). Para testar esta hipótesis, en un segundo paso se analizaron las correlaciones entre las distribuciones de las presas potenciales (principalmente, pequeños peces pelágicos) con las de sus depredadores, en este caso, cinco especies de aves marinas consideradas como prioritarias en nuestra zona de estudio. Para este estudio se utilizaron los resultados de las campañas de evaluación de pesquerías de pequeños peces pelágicos desarrolladas por el Instituto Español de Oceanografía, las cuales sirvieron de base a nuestro seguimiento de aves marinas.

En el análisis de las relaciones espaciales se utilizaron modelos lineales generalizados y modelos lineales generalizados mixtos. Los resultados demostraron que, de manera

general, la distribución de varias de las principales especies de aves marinas en el área de estudio se correlacionó con la de las especies sobre las que depredan, mientras que variables ambientales como la productividad primaria no mostraron relaciones biológicamente relevantes, ni con la distribución de las presas ni la de sus depredadores. Además, los análisis realizados mostraron que la distribución espacial de los depredadores y las presas solaparon en un porcentaje considerable. En particular, las tallas de tamaño medio de boquerón y sardina mostraron una alta correlación y un considerable solapamiento con la ocurrencia de especies como la pardela balear o el alcatraz atlántico en el Golfo de Cádiz. De esta manera, se demuestra que, al incorporar la distribución de las presas a los modelos de distribución de los depredadores, se obtienen resultados con un significado biológico más consistente (Kane *et al*., 2020).

Sin embargo, a pesar de ser estadísticamente significativos, no todos los modelos mostraron relaciones directas entre depredadores y presas. Especies como el paíño común, de hábitos más pelágicos y cuyo principal alimento es el krill o especies de pequeño tamaño (Albores-Barajas *et al*., 2011), mostraron una relación inversa con la distribución más costera de especies de peces de pequeña talla como los boquerones, a la vez que una relación negativa a la concentración de clorofila (con mayores concentraciones cerca de la costa). Por último, especies ampliamente distribuidas en el área de estudio, como es el caso de la pardela cenicienta (De la Cruz, 2013), o cuya distribución parece más determinada por la disponibilidad de descartes pesqueros como fuente de alimentación, como el caso de la gaviota de Audouin (Oro & Ruxton, 2001), no mostraron correlaciones con las presas sobre las que se alimenta.

La distribución espacial de cualquier especie no depende de un solo factor (Fauchald, 2009). No obstante, las relaciones encontradas entre las poblaciones de especies de aves marinas prioritarias, como la pardela balear y los pequeños peces pelágicos en el área de estudio, ponen de manifiesto la importancia de una adecuada evaluación y gestión de los stocks pesqueros para la conservación de las especies de depredadores marinos. Ante una situación de sobrepesca generalizada en prácticamente todos los caladeros del mundo (Frederiksen *et al*., 2004; Okes *et al*., 2009; Drago *et al*., 2018), la aparición de las AMP junto a la aplicación real de planes de gestión debe mejorar el estado de conservación general del mar, incrementar su biodiversidad e incluso hacer más productivos los caladeros de pesca (Hyrenbach *et al*., 2000; Hooker & Gerber, 2004). La combinación de campañas de evaluación pesquera

con estudios de depredadores marinos puede ser una metodología adecuada y rentable para abordar este problema y puede proporcionar información esencial para una ordenación de las pesquerías basada en un enfoque ecosistémico.

¿Cómo priorizar los esfuerzos en la gestión de un área marina protegida para la conservación de especies amenazadas?

Las AMP son una de las principales herramientas para la protección y conservación de las especies marinas. Sin embargo, la falta de planes de gestión o de su aplicación, junto a la ausencia de un seguimiento del cumplimiento de los objetivos por los que se declaran estas AMP, ponen en peligro la biodiversidad marina asociada a estas zonas y en particular a las aves marinas (Ronconi *et al*., 2012; European Green Party, 2019).

A modo de caso de estudio y aplicando modelos demográficos para mejorar la gestión de una especie amenazada en un área protegida, en el último capítulo de esta tesis doctoral se analizaron las presiones naturales y antropogénicas que sufre una pequeña población relicta de cormorán moñudo en un área marina portuguesa, la ZEPA Área Marina del Archipiélago de las Islas Berlengas. Los principales peligros identificados en la literatura para la supervivencia de esta especie fueron: la disponibilidad de presas suficientes; los eventos meteorológicos adversos durante el período en el que los pollos se encuentran aún en los nidos; la presencia de especies carnívoras invasoras, como las ratas; la mortalidad accidental asociada al *bycatch* por las diferentes artes de pesca; la presión turística durante la época de cría y los derrames de hidrocarburos derivados de accidentes de petroleros (Velando *et al*., 1999; Velando & Freire, 2002; Lilliendahl & Solmundsson, 2006; Silva, 2015; Fernandes, 2016; Genovart *et al*., 2017).

Para ello, se aplicaron modelos de dinámica de sistemas, considerados particularmente útiles por su diseño sencillo, continua mejora de software, aceptación por parte del usuario final, pero principalmente por la optimización de estrategias y medidas de gestión que ayudan a la toma de decisiones al gestor (Santos *et al*., 2013; Gillson *et al*., 2019). En base a este análisis, se predijo la respuesta de la población en la próxima década, tras proyectar diferentes estrategias de gestión ante las principales amenazas que sufre la especie en esta AMP. Entre todas las amenazas identificadas y en base a la aplicación de estos modelos, la mortalidad de individuos asociada a las ratas y al *bycatch* de la actividad pesquera destacaron sobre el resto.

Sin aplicar ningún tipo de estrategias de manejo, nuestras simulaciones mostraron un escenario donde la población de cormorán descendería un 7% en la próxima década. Sin embargo, si consiguiéramos aplicar medidas en las que se erradicaran las ratas en el archipiélago y no existiera mortalidad accidental durante la actividad pesquera, la población de cormorán en las Islas Berlengas podría verse aumentada en más de un 80% en los próximos años. La aplicación de medidas en esta dirección han mostrado resultados muy positivos en otras áreas marinas (Jouventin *et al*., 2003; Bell *et al*., 2016; Avery *et al*., 2017), por lo que nuestros resultados deberían ser considerados para su inmediata aplicación en la gestión del AMP.

Nuestros resultados pusieron una vez más de manifiesto la importancia de las interacciones entre las aves marinas y la pesca para la conservación. Si bien eliminar por completo el *bycatch* que produce la pesca es prácticamente imposible por las implicaciones socio-económicas de la pesca en una zona como las Islas Berlengas, es fundamental aplicar medidas que mitiguen o reduzcan esta causa de mortalidad del cormorán moñudo. Además, estas medidas también favorecerían a otras especies de aves marinas, como la amenazada pardela balear, la pardela cenicienta o el alcatraz atlántico, que visitan el AMP en diferentes épocas del año y que se ven afectadas por el *bycatch* de manera similar (Oliveira *et al*., 2020).

Los resultados de este tipo de modelos demográficos dinámicos demuestran que, considerando las múltiples amenazas coexistentes, la simulación de diferentes escenarios proyectados a futuro facilitan la toma de decisiones sobre las mejores opciones para la conservación de especies amenazadas en áreas marinas protegidas (Santos *et al*., 2013). En el caso de la ZEPA de las Islas Berlengas y con los resultados obtenidos, se hace necesario: 1) realizar un seguimiento de la población reproductora de cormorán moñudo bajo un enfoque ecosistémico, relacionando los datos demográficos de la población de cormoranes con las poblaciones de peces y las condiciones ambientales y meteorológicas; 2) controlar y erradicar la población de mamíferos invasores y actuar rápidamente ante posibles re-invasiones; 3) proponer y aplicar medidas de mitigación que reduzcan la mortalidad asociada al *bycatch* considerando incluso el cierre de las pesquerías durante ciertos períodos de tiempo; 4) reducir el número de turistas que visitan la ZEPA en la época reproductiva.

CONCLUSIONES
FINDINGS

CONCLUSIONES

En los diferentes trabajos expuestos en esta tesis doctoral se pone de manifiesto que la aplicación de modelos estadísticos sobre datos suficientemente consistentes de la distribución y la dinámica poblacional de especies paraguas puede contribuir de manera sustancial a la conservación y la gestión eficiente de zonas marinas con alto valor ecológico, como las áreas marinas protegidas (Pereira *et al*., 2018; Hawkes *et al*., 2019).

En nuestro caso, los depredadores apicales, como son las especies de aves marinas tratadas en los diferentes capítulos, forman un grupo idóneo para lograr este objetivo y podríamos confiar en que, conservando a las aves marinas, estamos conservando buena parte de los demás eslabones de la cadena trófica de la que forman parte (Zacharias & Roff, 2001). La preservación de estas especies juega un papel primordial en el conocimiento del estado de salud de nuestros mares y nuestras costas (Hunter *et al*., 2016), ya que el hecho de que este grupo de especies sea sensible a diferentes factores socio-ecológicos de naturaleza antropogénica, a competencia intra- e inter-específica, a especies invasoras, a cambios en las pesquerías, así como a alteraciones climáticas y oceanográficas, los hacen capaces de capturar la complejidad del ecosistema oceánico, sin dejar de ser lo suficientemente simple como para ser monitoreadas y estudiadas fácilmente (Siddig *et al*., 2016). La conservación de especies paraguas, como son las pardelas balear y cenicienta, los alcatraces, gaviotas, cormoranes o paíños, pueden llegar a representar la conservación de buena parte de su comunidad y del ecosistema marino que habitan.

Particularmente, las conclusiones alcanzadas en esta tesis doctoral han sido:

1. El área clave para la pardela balear en el Golfo de Cádiz se ha identificado en las áreas someras ubicadas entre la desembocadura del Guadalquivir y la zona marina frente a la Bahía de Cádiz, estando sólo parcialmente cubierta por la actual ZEPA Área Marina del Golfo de Cádiz (ES0000500) (<40%), lo que pone de manifiesto la urgencia de extender esta área marina protegida hacia el sureste para abarcar toda la superficie clave identificada.
2. Estudios a largo plazo junto a la toma de datos consistentes son imprescindibles para definir y evaluar la eficacia de las áreas marinas protegidas.

3. Variables abióticas, como la batimetría o la distancia al Guadalquivir, han resultado ser mejores predictores del hábitat esencial de la pardela balear frente a factores bióticos, como la concentración de clorofila, en ambientes oceánicos altamente dinámicos, lo que puede deberse al desfase espacio-temporal entre la producción primaria y los consumidores.
4. El uso conjunto de diferentes técnicas de modelado espacial, utilizando conjuntos de datos suficientemente amplios, ofrece resultados robustos y consistentes en la predicción de la distribución de especies de aves marinas como la pardela balear.
5. La distribución de las principales especies de aves marinas en el Golfo de Cádiz está correlacionada y altamente solapada con la de sus presas naturales, particularmente de pequeños peces pelágicos.
6. De manera particular, la distribución de especies tan importantes como la críticamente amenazada pardela balear se encuentra determinada en el Golfo de Cádiz por la presencia de boquerón y sardina de talla mediana.
7. La integración de información dispersa de una especie amenazada, como el cormorán moñudo en la ZEPA Área Marina del Archipiélago de las Islas Berlengas (PTZPE0009), mediante la aplicación de modelos demográficos y dinámica de sistemas ofrece una de las herramientas más eficaces en la gestión de las áreas marinas protegidas.
8. Entre todas las presiones identificadas, las especies de carnívoros invasores como las ratas y la mortalidad asociada a la captura accidental por la actividad pesquera en el área de estudio son las principales amenazas del cormorán moñudo. Estas amenazas provocarían una disminución del 7% de la población de cormorán moñudo en la ZEPA de las Islas Berlengas en la próxima década si no se aplicara ninguna medida de gestión. Sin embargo, la población puede verse altamente favorecida si se mantiene el archipiélago libre de carnívoros invasores y se aplican medidas de mitigación para reducir la muerte de cormorán moñudo por *bycatch*.

FINDINGS

In the different research presented in this thesis it is shown that the application of statistical models on sufficiently consistent data of the distribution and population dynamics of umbrella species can substantially contribute to the conservation and efficient management of marine areas of high ecological value, such as marine protected areas (Pereira *et al*., 2018; Hawkes *et al*., 2019).

In our case, top predators, such as the seabirds species discussed in the different chapters, conform an ideal group to achieve this objective. We can trust that, by conserving seabirds, we are conserving a large part of the links in the trophic chain of which they are part (Zacharias & Roff, 2001). The preservation of these species plays a fundamental role in understanding the state of health of our seas and our coasts (Hunter *et al*., 2016), since this group of species is sensitive to different socio-ecological factors of anthropogenic nature, intra- and interspecific competition, invasive species, changes in fisheries or climatic and oceanographic alterations. These features make them capable of capturing the complexity of the oceanic ecosystem, while remaining simple enough to be monitored and studied easily (Siddig *et al*. 2016). The conservation of umbrella species, such as shearwaters, gannets, gulls, cormorants or storm-petrels, can represent the conservation of a large part of their community and the marine ecosystem they inhabit.

In particular, the conclusions reached in this doctoral thesis have been:

1. The key area for the Balearic shearwater in the Gulf of Cádiz has been identified as being the shallow areas located between the mouth of the Guadalquivir River and the marine area off the Bay of Cádiz, being only partially covered by the current Gulf of Cadiz Marine Area SPA (ES0000500) (<40%). This highlights the urgency of extending this marine protected area to the southeast to cover the entire identified key area.
2. Long-term studies together with the collection of consistent data are essential to define and evaluate the effectiveness of marine protected areas.

3. Abiotic variables, such as bathymetry or distance to the Guadalquivir River, have proven to be better predictors of the essential habitat of the Balearic shearwater compared to biotic factors, such as chlorophyll concentration, in highly dynamic oceanic environments, which may be due to spatio-temporal lag between primary production and consumers.
4. The joint use of different spatial modelling techniques, using sufficiently large data sets, offers robust and consistent results in the prediction of the distribution of seabird's species such as the Balearic shearwater.
5. The distribution of the main species of seabirds in the Gulf of Cádiz is highly correlated and overlapped with that of their natural prey, particularly small pelagic fish.
6. In particular, the distribution of priority species as the critically endangered Balearic shearwater is determined in the Gulf of Cádiz by the presence of medium-sized anchovies and sardines.
7. The integration of dispersed information on a threatened species, such as Shag in the Berlengas Archipelago Marine Area SPA (PTZPE0009), through the application of demographic models and system dynamics, offers one of the most effective tools in the management of marine protected areas.
8. Among all the pressures identified, invasive carnivore species such as rats and mortality associated with accidental capture due to fishing activity in the study area are the main threats to the Shag. These threats would cause a 7% decrease in the species population in the Berlengas SPA in the next decade without applying any management measures. However, the population could be highly favoured if the archipelago is kept free of invasive carnivores and mitigation measures are applied to reduce Shag predation and bycatch.

MATERIAL SUPLEMENTARIO

Table A.1. Summer oceanographic campaign details throughout years on board the vessel of IEO.

Year campaign	Dates	Days	No. survey units	Average survey lenght (km)
2006	19-30 June	12	133	410.53
2007	3-11 July	9	205	632.77
2009	27-30 June & 2-8 July	11	167	515.47
2010	26-31 July	6	132	407.44
2013	2-11 August	10	312	963.04
2014	24-31 July & 1-4 August	12	170	524.73
2015	29-31 July & 1-8 August	11	195	601.9
2016	31 July & 1-10 August	11	189	583.38
2017	1-11 August	11	263	811.79

Table A.2. 50% utilization distribution contour polygons characteristics of all years surveyed in the Gulf of Cadiz for the BSH.

Year	KDE 50 Polygons	KDE 50 Area (km^2)	Overlap with SPA (%)	Dist. to Coast (km)	Lat centroid	Lon centroid
2006	2006-1	1956.9	0.55	20.3	36.70	-6.67
2007	2007-1	173			37.00	-8.44
	2007-2	2024.7	0.72	26.7	36.76	-6.74
2009	2009-1	218.4	No overlap	8.4	36.92	-8.02
	2009-2	443.7	0.74	13.6	36.98	-6.80
	2009-3	1411.3	0.12	19.3	36.48	-6.54
2010	2010-1	215.9	0.92	13.8	37.08	-7.14
	2010-2	831.7	0.84	22.3	36.79	-6.69
	2010-3	117.6	No overlap	7.4	36.43	-6.37
2013	2013-1	1309.4	0.25	20.3	36.51	-6.56
2014	2014-1	1389.9	0.30	15.6	36.57	-6.56
2015	2015-1	1803.4	0.96	28.2	36.86	-6.89
2016	2016-1	154.7			36.56	-8.19
	2016-2	2098.6	No overlap	17.2	36.22	-6.31
2017	2017-1	1204.7	0.82	28.3	36.95	-7.12
	2017-2	554	0.14	18.6	36.51	-6.53

Table S1. Summer survey details throughout years on-board IEO's research vessel. Dates and days of every year, lineal transect covered annually and total number of 10 minutes survey units are shown.

Year survey	Dates	Days of survey	Nº Survey units	Average sample distance (km)
2006	19-30 June	12	133	410.53
2007	3-11 July	9	205	632.77
2009	27-30 June & 2-8 July	11	167	515.47
2010	26-31 July	6	132	407.44
2013	2-11 August	10	312	963.04
2014	24-31 July & 1-4 August	12	170	524.73
2015	29-31 July & 1-8 August	11	195	601.9
2016	31 July & 1-10 August	11	189	583.38
2017	1-11 August	11	263	811.79
2018	1-11 August	11	237	731.54

Table S2. Variables considered and proxy description for the BSH suitable habitat modelling process with 4 km^2 resolution.

Variable		Description as a proxy of	Source
Bathymetry	bat	Depth water requirements, physical processes driving prey distribution	EMODnet (Marine Information Service 2016)
Slope	slope	Potential upwelling occurrence	Derived from EMODnet (Marine Information Service 2016) using ArcGis (ESRI, 2016)
Distance to 50 m isobath	iso50	Depth water requirements, physical processes driving prey distribution	Derived from EMODnet (Marine Information Service 2016)
Distance to 100 m isobath	Iso1000	Depth water requirements, physical processes driving prey distribution	Derived from EMODnet (Marine Information Service 2016)
Distance to 200 m isobath	iso200	Shelf Break; depth water requirements, physical processes driving prey distribution and potential upwelling occurrence	Derived from EMODnet (Marine Information Service 2016)
Distance to 500 m isobath	iso500	Depth water requirements, physical processes driving prey distribution	Derived from EMODnet (Marine Information Service 2016)
Distance to 1000 m isobath	iso1000	Depth water requirements, physical processes driving prey distribution	Derived from EMODnet (Marine Information Service 2016)
Distance to coast line	d_coast	Coastal vs. Pelagic behaviour	Calculated using ArcGIS (ESRI, 2016)
Distance to Tinto & Odiel river mouth	d_tinOd	Potential source of organic matter	Calculated using ArcGIS (ESRI, 2016)
Distance to Guadiana river mouth	d_guadi	Potential source of organic matter	Calculated using ArcGIS (ESRI, 2016)
Distance to Guadalquivir river mouth	d_gua-dalq	Potential source of organic matter	Calculated using ArcGIS (ESRI, 2016)
Distance to Guadalete river mouth	d_gua-dele	Potential source of organic matter	Calculated using ArcGIS (ESRI, 2016)
Chlorophyll a concentration	CHL	Primary productivity	Monthly Aqua-MODIS Satellite imagery spatial resolution 4 km^2
Sea Surface Temperature	SST	Water mass distribution and prey distribution	Monthly Aqua-MODIS Satellite imagery spatial resolution 4 km^2
Turbidity	TSM	Suspended solid – Organic Matter - Marine productivity	Derived from Remote Sensing Reflectance following Caballero *et al.*, 2014. Aqua-MODIS Resolution 4 km^2

Table S3. Bivariate Spearman rank p-values and correlations between vessel-related variables analysed in the GLMMs. Highly correlated (|rs| > 0.65) predictors are marked in bold and shaded. † Variables selected for the modelling process.

	†Bat	**†CHL**	D_Coast	D_Guadale	**†D_Guadalq**	**†D_Guadi**	Iso50	Iso100	Iso500	Iso1000	**†Iso200**	D_TinOd	Slope	**†SST**	TSM
† Bat	-	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001
† CHL	0.64	-	<.0001	0.00	0.01	0.00	<.0001	0.00	<.0001	0.00	<.0001	0	<.0001	<.0001	<.0001
D_Coast	-0.71	-0.76	-	0.00	<.0001	0.02	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001
D_Guadale	-0.38	0.08	-0.07	-	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001
† D_Guadalq	-0.39	0.06	-0.11	0.91	-	0.59	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001
† D_Guadi	0.11	0.07	-0.05	-0.27	0.01	-	0.57	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	0.08	0.04
Iso50	-0.66	-0.45	0.60	0.16	0.16	0.01	-	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001	0.19	<.0001
Iso100	0.26	0.07	-0.08	-0.19	-0.18	0.14	0.16	-	<.0001	<.0001	<.0001	0.04	<.0001	<.0001	<.0001
Iso500	0.81	0.39	-0.36	-0.57	-0.61	0.14	-0.44	0.41	-	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001
Iso1000	0.71	0.32	-0.34	-0.62	-0.64	-0.19	-0.42	0.21	0.75	-	<.0001	0.04	<.0001	<.0001	<.0001
† Iso200	0.60	0.24	-0.30	-0.32	-0.33	0.12	-0.25	0.74	0.74	0.46	-	<.0001	<.0001	<.0001	<.0001
D_TinOd	-0.22	0.08	-0.16	0.41	0.67	0.70	0.11	-0.05	-0.39	-0.66	-0.17	-	<.0001	<.0001	0.00
Slope	-0.71	-0.41	0.41	0.42	0.43	-0.12	0.41	-0.20	-0.69	-0.59	-0.54	0.25	-	<.0001	<.0001
† SST	0.13	-0.35	0.16	-0.45	-0.45	-0.04	-0.03	0.19	0.27	0.29	0.27	-0.32	-0.17	-	<.0001
TSM	0.68	0.80	-0.67	-0.16	-0.18	0.05	-0.41	0.16	0.48	0.46	0.32	-0.08	-0.45	-0.17	-

Table S4. Biologically relevant explanatory variables used for BSH distribution modelling and associated oceanographic processes. Shaded model (mod28) indicate the best model of the BSH occurrence in the GoC. Only models with significant variables are presented in the table with their AIC (Akaike Information Criterion) value. log_bat indicate logarithm base 10 of bathymetry in meters, log d_guadalq indicate logarithm base 10 of Euclidean distance from Guadalquivir river mouth in meters; CHL indicate chlorophyll-a concentration in mg m-3, log_d_plat indicate Euclidean distance from the 200 m isobath in meters, SST indicate the sea surface temperature in °C. df.resid: Residuals degrees of freedom.

#Model	Single variables	Estimate	Std. Error	deviance	df.resid	p Value	AIC
mod01	log_bat	-1.47	0.18	1960.1	2108	<0.001	1966.1
mod02	log_guadi	0	0.22	2036.9	2108	0.99	2042.9
mod03	log_guadalq	-1.75	0.21	1964	2108	<0.001	1970
mod04	log_iso200	0.84	0.13	1991.2	2108	<0.001	1997.2
mod05	CHL	0.29	0.09	2027.3	2108	0.00	2033.3
mod06	SST	0.11	0.05	2031	2108	0.02	2037
mod07	log_bat	-1.47	0.18	1960.1	2107	<0.001	1968.1
	log_guadi	-0.06	0.21			0.78	
mod08	log_bat	-1.1	0.19	1927.7	2107	<0.001	1935.7
	log_guadalq	-1.23	0.22			<0.001	
mod09	log_bat	-1.26	0.24	1958.6	2107	<0.001	1966.6
	log_iso200	0.22	0.17			0.21	
mod10	log_bat	1.57	0.44	1958.9	2107	<0.001	1966.9
	CHL	-1.57	0.2			<0.001	
mod11	log_bat	-1.45	0.18	1960	2107	<0.001	1968
	SST	0.01	0.05			0.76	
mod12	log_guadi	-0.19	0.23	1963.3	2107	0.41	1971.3
	log_guadalq	-1.78	0.21			<0.001	
mod13	log_guadi	-0.21	0.22	1990.3	2107	0.34	1998.3
	log_iso200	0.86	0.14			<0.001	
mod14	log_guadi	-0.06	0.22	2027.3	2107	0.77	2035.3
	CHL	0.29	0.09			0.00	

Table S4. (Cont..)

#Model	Single variables	Estimate	Std. Error	deviance	df.resid	p Value	AIC
mod15	log_guadi	0.02	0.22	2031	2107	0.92	2039
	SST	0.11	0.05			0.02	
mod16	log_guadalq	-1.47	0.22	1942.1	2107	<0.001	1950.1
	log_iso200	0.6	0.13			<0.001	
mod17	log_guadalq	-1.83	0.21	1946.1	2107	<0.001	1954.1
	CHL	0.41	0.1			<0.001	
mod18	log_guadalq	-2.37	0.27	1949.8	2107	<0.001	1957.8
	SST	-0.23	0.06			<0.001	
mod19	log_iso200	0.8	0.14	1990.3	2107	<0.001	1998.3
	CHL	0.1	0.1			0.32	
mod20	log_iso200	0.81	0.13	1989.6	2107	<0.001	1997.6
	SST	0.06	0.05			0.20	
mod21	CHL	0.34	0.09	2018.5	2107	<0.001	2026.5
	SST	0.14	0.05			0.00	
mod22	log_bat	-1.1	0.19	1926.9	2106	<0.001	1936.9
	log_guadi	-0.19	0.22			0.40	
	log_guadalq	-1.25	0.22			<0.001	
mod23	log_bat	-1.24	0.24	1958.3	2106	<0.001	1968.3
	log_guadi	-0.11	0.22			0.61	
	log_iso200	0.23	0.18			0.19	
mod24	log_bat	-1.57	0.2	1958.9	2106	<0.001	1968.9
	log_guadi	-0.04	0.21			0.84	
	CHL	-0.12	0.11			0.29	

Table S4. (Cont..)

#Model	Single variables	Estimate	Std. Error	deviance	df.resid	p Value	AIC
mod25	log_bat	-1.46	0.18	1960	2106	<0.001	1970
	log_guadi	-0.06	0.21			0.79	
	SST	0.01	0.05			0.76	
mod26	log_bat	-0.93	0.25	1926.5	2106	<0.001	1936.5
	log_guadalq	-1.22	0.22			<0.001	
	log_iso200	0.18	0.17			0.29	
mod27	log_bat	-0.98	0.22	1926.6	2106	<0.001	1936.6
	log_guadalq	-1.31	0.24			<0.001	
	CHL	0.12	0.12			0.30	
mod28	log_bat	-1.12	0.19	1913.4	2106	<0.001	1923.4
	log_guadalq	-1.83	0.28			<0.001	
	SST	-0.23	0.06			<0.001	
mod29	log_bat	-1.35	0.26	1957.3	2106	<0.001	1967.3
	log_iso200	0.22	0.17			0.20	
	CHL	-0.12	0.11			0.27	
mod30	log_bat	-1.24	0.24	1958.5	2106	<0.001	1968.5
	log_iso200	0.22	0.17			0.21	
	SST	0.01	0.05			0.77	
mod31	log_bat	-1.57	0.21	1958.9	2106	<0.001	1968.9
	CHL	-0.12	0.12			0.30	
	SST	0	0.05			0.97	
mod32	log_guadi	-0.3	0.23	1940.3	2106	0.18	1950.3
	log_guadalq	-1.5	0.22			<0.001	
	log_iso200	0.62	0.14			<0.001	

Table S4. (Cont..)

#Model	Single variables	Estimate	Std. Error	deviance	df.resid	p Value	AIC
mod33	log_guadi	-0.27	0.23	1944.6	2106	0.22	1954.6
	log_guadalq	-1.87	0.21			<0.001	
	CHL	0.43	0.1			<0.001	
mod34	log_guadi	-0.26	0.23	1948.5	2106	0.26	1958.5
	log_guadalq	-2.42	0.28			<0.001	
	SST	-0.23	0.06			<0.001	
mod35	log_guadi	-0.22	0.22	1989.2	2106	0.31	1999.2
	log_iso200	0.82	0.14			<0.001	
	CHL	0.1	0.1			0.29	
mod36	log_guadi	-0.19	0.22	1988.8	2106	0.38	1998.8
	log_iso200	0.83	0.14			<0.001	
	SST	0.06	0.05			0.22	
mod37	log_guadi	-0.04	0.22	2018.5	2106	0.84	2028.5
	CHL	0.34	0.1			<0.001	
	SST	0.14	0.05			0.00	
mod38	log_guadalq	-1.59	0.22	1935	2106	<0.001	1945
	log_iso200	0.46	0.14			0.00	
	CHL	0.28	0.1			0.01	
mod39	log_guadalq	-2.09	0.28	1927.8	2106	<0.001	1937.8
	log_iso200	0.6	0.13			<0.001	
	SST	-0.23	0.06			<0.001	
mod40	log_guadalq	-2.38	0.27	1934.7	2106	<0.001	1944.7
	CHL	0.39	0.1			<0.001	
	SST	-0.21	0.06			<0.001	

Table S4. (Cont.)

#Model	Single variables	Estimate	Std. Error	deviance	df.resid	p Value	AIC
mod41	log_iso200	0.75	0.14	1987.8	2106	<0.001	1997.8
	CHL	0.13	0.1			0.18	
	SST	0.07	0.05			0.12	
mod42	log_bat	-0.9	0.25	1925.5	2105	<0.001	1937.5
	log_guadi	-0.23	0.22			0.31	
	log_guadalq	-1.25	0.22			<0.001	
	log_iso200	0.21	0.17			0.23	
mod43	log_bat	-0.96	0.22	1925.7	2105	<0.001	1937.7
	log_guadi	-0.21	0.22			0.34	
	log_guadalq	-1.35	0.24			<0.001	
	CHL	0.13	0.12			0.26	
mod44	log_bat	-1.12	0.19	1912.1	2105	<0.001	1924.1
	log_guadi	-0.26	0.23			0.25	
	log_guadalq	-1.88	0.28			<0.001	
	SST	-0.23	0.06			<0.001	
mod45	log_bat	-1.34	0.26	1957.1	2105	<0.001	1969.1
	log_guadi	-0.09	0.22			0.67	
	log_iso200	0.23	0.18			0.18	
	CHL	-0.12	0.11			0.29	
mod46	log_bat	-1.23	0.24	1958.2	2105	<0.001	1970.2
	log_guadi	-0.11	0.22			0.62	
	log_iso200	0.23	0.18			0.19	
	SST	0.01	0.05			0.78	

Table S4. (Cont.)

#Model	Single variables	Estimate	Std. Error	deviance	df.resid	p Value	AIC
mod47	log_bat	-1.57	0.21	1958.9	2105	<0.001	1970.9
	log_guadi	-0.04	0.21			0.84	
	CHL	-0.12	0.12			0.31	
	SST	0	0.05			0.97	
mod48	log_bat	-0.81	0.27	1925.5	2105	0.00	1937.5
	log_gua-dalq	-1.3	0.24			<0.001	
	log_iso200	0.18	0.17			0.30	
	CHL	0.12	0.12			0.31	
mod49	log_bat	-0.94	0.25	1912.3	2105	<0.001	1924.3
	log_gua-dalq	-1.83	0.28			<0.001	
	log_iso200	0.18	0.17			0.30	
	SST	-0.23	0.06			<0.001	
mod50	log_bat	-1.05	0.23	1913.1	2105	<0.001	1925.1
	log_gua-dalq	-1.87	0.29			<0.001	
	CHL	0.07	0.12			0.58	
	SST	-0.22	0.06			<0.001	
mod51	log_bat	-1.36	0.26	1957.3	2105	<0.001	1969.3
	log_iso200	0.22	0.17			0.20	
	CHL	-0.12	0.12			0.29	
	SST	0	0.05			0.95	
mod52	log_guadi	-0.34	0.23	1932.8	2105	0.14	1944.8
	log_gua-dalq	-1.63	0.22			<0.001	
	log_iso200	0.48	0.14			<0.001	
	CHL	0.29	0.1			0.01	

Table S4. (Cont..)

#Model	Single variables	Estimate	Std. Error	deviance	df.resid	p Value	AIC
mod53	log_guadi	-0.38	0.23	1925.1	2105	0.10	1937.1
	log_guadalq	-2.15	0.28			<0.001	
	log_iso200	0.62	0.14			<0.001	
	SST	-0.24	0.06			0	
mod54	log_guadi	-0.34	0.23	1932.5	2105	0.14	1944.5
	log_guadalq	-2.45	0.28			<0.001	
	CHL	0.4	0.1			<0.001	
	SST	-0.21	0.06			<0.001	
mod55	log_guadi	-0.2	0.22	1987	2105	0.35	1999
	log_iso200	0.76	0.14			<0.001	
	CHL	0.14	0.1			0.17	
	SST	0.07	0.05			0.14	
mod56	log_guadalq	-2.15	0.28	1922.6	2105	<0.001	1934.6
	log_iso200	0.48	0.14			<0.001	
	CHL	0.24	0.1			0.02	
	SST	-0.21	0.06			<0.001	
mod57	log_bat	-0.77	0.27	1924.3	2104	0.01	1938.3
	log_guadi	-0.25	0.22			0.26	
	log_guadalq	-1.34	0.24			<0.001	
	log_iso200	0.2	0.17			0.24	
	CHL	0.13	0.12			0.27	

Table S4. (Cont.)

#Model	Single variables	Estimate	Std. Error	deviance	df.resid	p Value	AIC
mod58	log_bat	-0.91	0.25	1910.6	2104	<0.001	1924.6
	log_guadi	-0.3	0.23			0.19	
	log_guadalq	-1.88	0.28			<0.001	
	log_iso200	0.21	0.17			0.23	
	SST	-0.24	0.06			<0.001	
mod59	log_bat	-1.03	0.23	1911.6	2104	<0.001	1925.6
	log_guadi	-0.28	0.23			0.22	
	log_guadalq	-1.92	0.29			<0.001	
	CHL	0.08	0.12			0.50	
	SST	-0.23	0.06			<0.001	
mod60	log_bat	-1.34	0.27	1957.1	2104	<0.001	1971.1
	log_guadi	-0.09	0.22			0.67	
	log_iso200	0.23	0.18			0.18	
	CHL	-0.12	0.12			0.3	
	SST	0	0.05			0.95	
mod61	log_bat	-0.87	0.28	1912.1	2104	0.00	1926.1
	log_guadalq	-1.86	0.29			<0.001	
	log_iso200	0.18	0.17			0.31	
	CHL	0.06	0.12			0.59	
	SST	-0.22	0.06			<0.001	
mod62	log_guadi	-0.41	0.23	1919.5	2104	0.08	1933.5
	log_guadalq	-2.22	0.28			<0.001	
	log_iso200	0.5	0.14			<0.001	
	CHL	0.25	0.11			0.02	
	SST	-0.22	0.06			<0.001	

Table S4. (Cont.)

#Model	Single variables	Estimate	Std. Error	deviance	df.resid	p Value	AIC
mod63	log_bat	-0.83	0.28	1910.2	2103	0.00	1926.2
	log_guadi	-0.32	0.23			0.17	
	log_guadalq	-1.92	0.29			<0.001	
	log_iso200	0.21	0.17			0.23	
	CHL	0.08	0.12			0.50	
	SST	-0.23	0.06			<0.001	

S1. Bivariate Spearman rank p-values and correlations between considered bird and fish species and environmental variables included as variables analysed in the models. Highly correlated (|rs| > 0.65) predictors are marked shaded. CALBOR: Cory's shearwater *Calonectris borealis*, HYDPEL: European storm-petrel *Hydrobates pelagicus*, ICHAUD: Audouin's gull *Ichthyaetus audouinii*, PUFMAU: Balearic shearwater *Puffinus mauretanicus*, MORBAS: Northern gannet *Morus bassanus*. ANE: European anchovy *Engraulis encrasicolus*, PIL: European pilchard *Sardina pilchardus*, MAC: Atlantic mackerel *Scomber scombrus*, MAS: Chub mackerel *Scomber colias*, HOM: Atlantic horse mackerel *Trachurus trachurus*, HMM: Mediterranean horse mackerel *Trachurus mediterraneus*, JAA: Blue jack mackerel *Trachurus picturatus* and BOG: Bogue *Boops boops*. SMA_group, MED_group, LAR_group are the sum of the abundance of all the small, medium and large size individuals respectively.

	CALBOR	HYDPEL	LARAUD	MORBAS	PUFMAU	CHL	SST	TSM
CALBOR								
HYDPEL	0.03							
LARAUD	0.01	0.01						
MORBAS	0.07*	-0.08*	0.06					
PUFMAU	0.09**	0.16***	0.06	0.03				
CHL	0.05	-0.10**	0.09**	0.31***	-0.03			
SST	-0.08*	0.02	0.02	-0.11**	0.08*	-0.35***		
TSM	-0.01	-0.14***	0.11***	0.22***	0.07*	0.80***	-0.13***	
ANE_PEQ	-0.05	-0.12***	-0.02	-0.01	0.18***	-0.04	0.30***	0.13***
HOM_PEQ	0.07*	0.01	0.02	0.03	0.10**	0.12***	-0.29***	0.15***
PIL_PEQ	-0.08*	-0.09**	0.04	0.01	0.13***	-0.09**	0.36***	0.07*
ANE_MED	0.04	-0.11**	0.04	0	0.14***	-0.17***	0.23***	-0.01
BOG_MED	-0.07*	-0.09**	0.02	0.21***	0.01	0.24***	-0.14***	0.13***
HMM_MED	-0.01	-0.03	0.02	0.06	0.19***	-0.08*	0.09**	-0.01
HOM_MED	0	-0.04	0.04	0.14***	-0.04	0.26***	-0.29***	0.16***
JAA_MED	0.02	0.04	0.01	0.09**	-0.11***	0.14***	-0.37***	-0.04
MAC_MED	-0.08*	-0.07*	-0.04	-0.11**	-0.09**	0.01	0.04	0.11***
MAS_MED	0.03	0.02	0	0.09**	-0.11***	-0.02	-0.02	-0.26***
PIL_MED	0.01	-0.08*	0.13***	0.18***	0.14***	0.21***	0.19***	0.26***
BOG_GRA	-0.09**	-0.05	0.04	0.19***	0.07*	0.17***	0.04	0.11**
HMM_GRA	-0.07*	-0.10**	0.03	0.07*	0.17***	-0.01	0.34***	0.17***
HOM_GRA	-0.03	-0.02	-0.01	0.14***	-0.09**	0.28***	-0.34***	0.13***
JAA_GRA	-0.01	0.03	-0.06	0.05	-0.10**	0.12***	-0.39***	-0.06
MAC_GRA	0.08*	0.02	0.02	-0.04	0.11**	-0.23***	0.15***	-0.16***
MAS_GRA	0.06	-0.04	0.04	0.13***	-0.10**	0.12***	-0.16***	-0.12***
PIL_GRA	-0.05	-0.01	-0.01	0.05	-0.09**	0.16***	-0.13***	0.07*
SMA	-0.04	-0.11***	0.02	0.01	0.23***	-0.06	0.26***	0.12***
MED	0.08*	-0.10**	0.08*	0.12***	0.11**	0.04	0.13***	0.08*
LAR	0.05	-0.07*	0.03	0.16***	0	0.14***	-0.08*	-0.01

Table S1.(Cont.)

	ANE_PEQ	HOM_PEQ	PIL_PEQ	ANE_MED	BOG_MED	HMM_MED	HOM_MED	JAA_MED	MAC_MED	MAS_MED	PIL_MED
HOM_PEQ	0.21***										
PIL_PEQ	0.48***	0.05									
ANE_MED	0.40***	0.13***	0.44***								
BOG_MED	-0.09**	-0.01	0.04	-0.05							
HMM_MED	-0.04	-0.07*	0.22***	0.09**	0.28***						
HOM_MED	-0.01	0.51***	0.06	0.01	0.42***	-0.12***					
JAA_MED	-0.27***	0.28***	-0.27***	-0.08*	0.29***	-0.12***	0.42***				
MAC_MED	-0.10**	-0.14***	0.01	0.29***	-0.04	-0.08*	0.04	-0.04			
MAS_MED	-0.24***	-0.11***	-0.08*	0.06	0.29***	-0.13***	0.30***	0.36***	0.02		
PIL_MED	0.30***	0.20***	0.48***	0.46***	0.24***	0.12***	0.38***	-0.09**	0.04	0.17***	
BOG_GRA	0.11***	0.09**	0.42***	0.22***	0.70***	0.22***	0.48***	0.21***	0.03	0.38***	0.49***
HMM_GRA	0.40***	-0.12***	0.53***	0.25***	0.02	0.39***	-0.14***	-0.25***	-0.14***	-0.15***	0.34***
HOM_GRA	-0.24***	0.12***	-0.11***	-0.03	0.52***	-0.10**	0.73***	0.56***	0.13***	0.40***	0.24***
JAA_GRA	-0.25***	0.22***	-0.20***	-0.14***	0.33***	-0.10**	0.35***	0.78***	0	0.37***	-0.16***
MAC_GRA	0.08*	0.10**	0.15***	0.52***	0.01	0.13***	0.14***	-0.07*	0.36***	0.08*	0.29***
MAS_GRA	-0.34***	-0.03	-0.10**	0.13***	0.42***	0.14***	0.33***	0.46***	0.10**	0.75***	0.20***
PIL_GRA	-0.02	0.39***	0.01	0.02	0.11***	-0.09**	0.45***	0.29***	0.01	0.30***	0.25***
SMA	0.79***	0.40***	0.74***	0.52***	0.02	0.14***	0.17***	-0.16***	-0.10**	-0.17***	0.52***
MED	0.25***	0.11***	0.36***	0.78***	0.17***	0.04	0.27***	0.06	0.24***	0.38***	0.69***
LAR	-0.06	0.09**	0.09**	0.26***	0.48***	0.17***	0.39***	0.42***	0.01	0.57***	0.34***

Table S1.(Cont.)

	BOG_GRA	HMM_GRA	HOM_GRA	JAA_GRA	MAC_GRA	MAS_GRA	PIL_GRA	SMA	MED
HMM_GRA	0.29***								
HOM_GRA	0.51***	-0.16***							
JAA_GRA	0.30***	-0.23***	0.55***						
MAC_GRA	0.12***	-0.12***	0.07*	-0.17***					
MAS_GRA	0.41***	-0.08*	0.47***	0.47***	0.12***				
PIL_GRA	0.24***	0	0.33***	0.28***	-0.13***	0.29***			
SMA	0.30***	0.49***	-0.08*	-0.13***	0.18***	-0.17***	0.16***		
MED	0.43***	0.18***	0.23***	-0.03	0.48***	0.42***	0.13***	0.40***	
LAR	0.58***	0.24***	0.50***	0.44***	0.16***	0.79***	0.29***	0.13***	0.52***

Appendix I. Stella software conceptual diagrams of the model used to predict Shag dynamics in the Berlengas SPA

Population dynamics sub-models

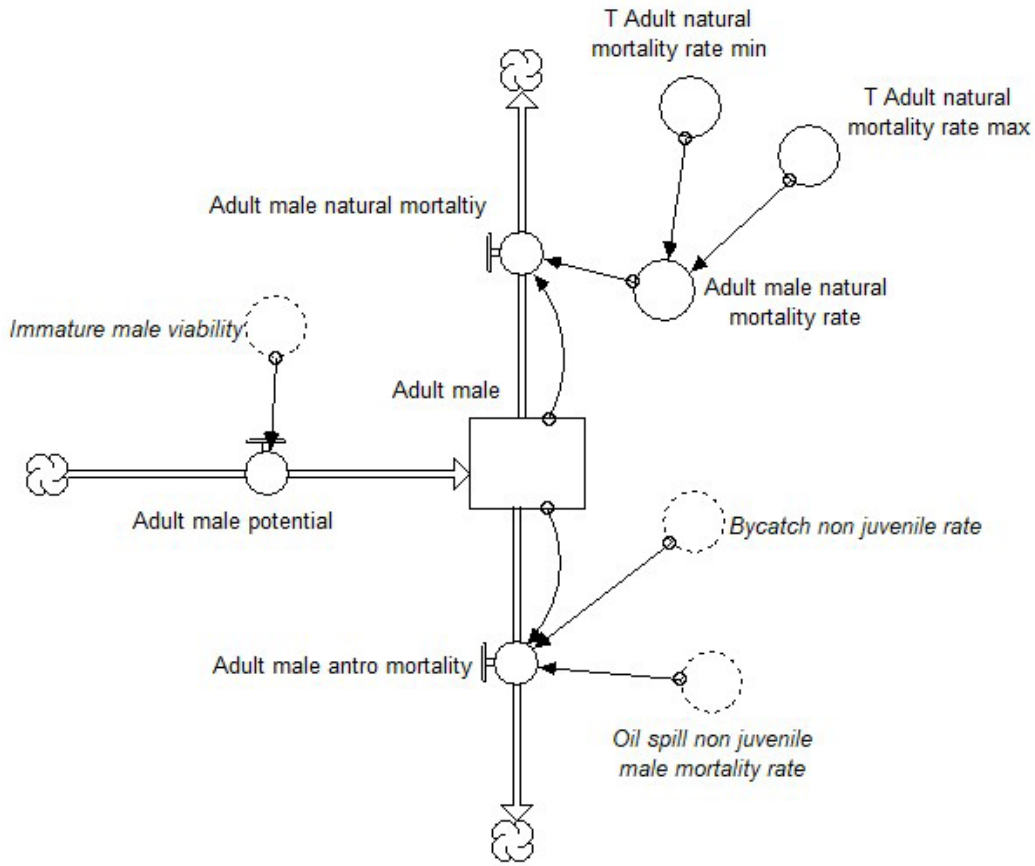


Figure S1. Stella software conceptual diagram of the sub-model of Adult male dynamics. Rectangles represent the state variables: Adult male; other variables, parameters or constants are small circles; sinks and sources are cloudlike symbols; flows are thick arrows; all the relations between state variables and other variables are fine arrows. The specification of all variable codes is expressed in Appendix II and main description in Table 1 of the manuscript.

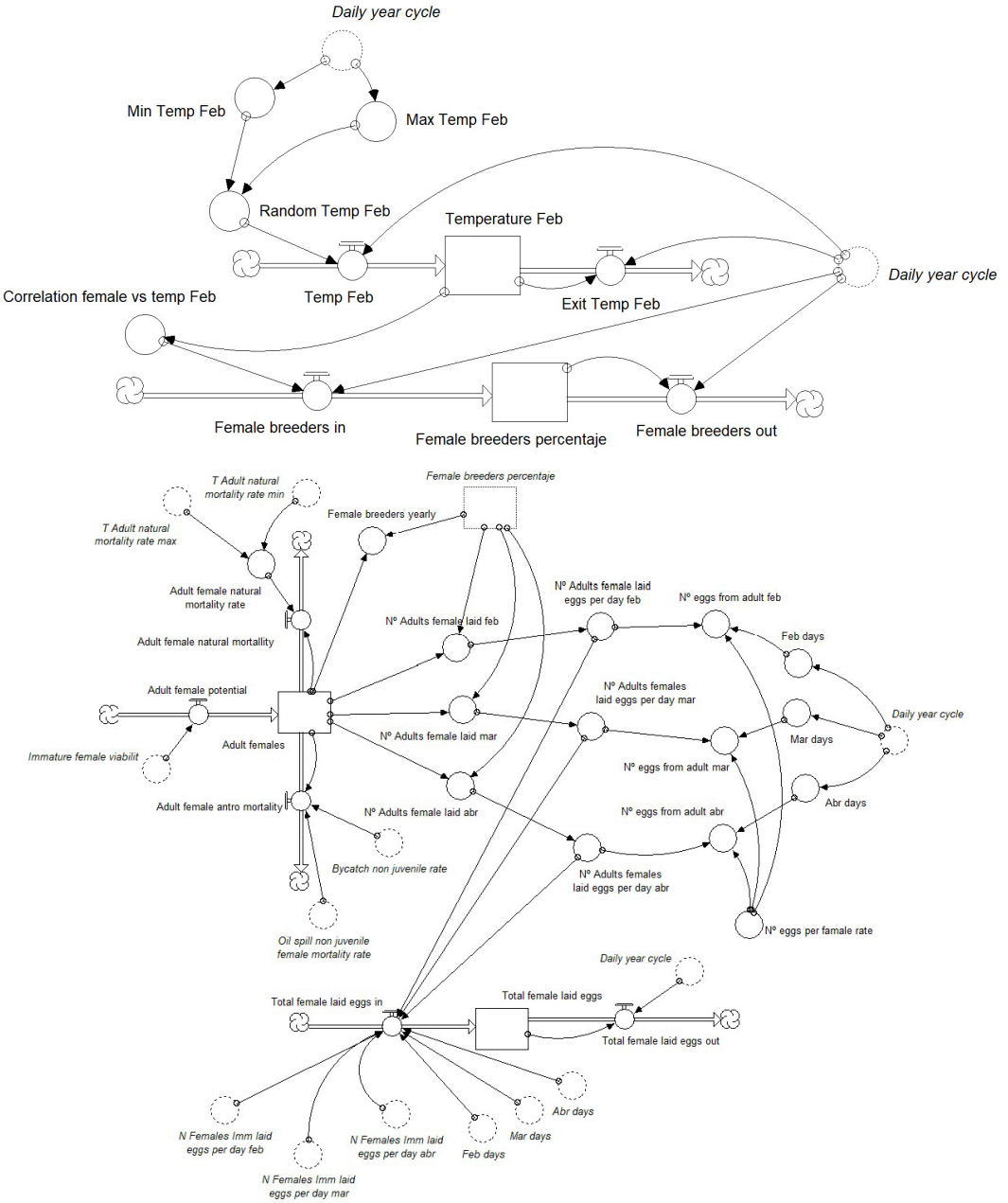


Figure S2. Stella software conceptual diagram of the sub-model of Adult female and breeding dynamics. Rectangles represent the state variables: February Temperature, Percentage of breeding females, Adult female and Total eggs laid; other variables, parameters or constants are small circles; sinks and sources are cloudlike symbols; flows are thick arrows; all the relations between state variables and other variables are fine arrows. The specification of all variable codes is expressed in Appendix II and main description in Table 1 of the manuscript.

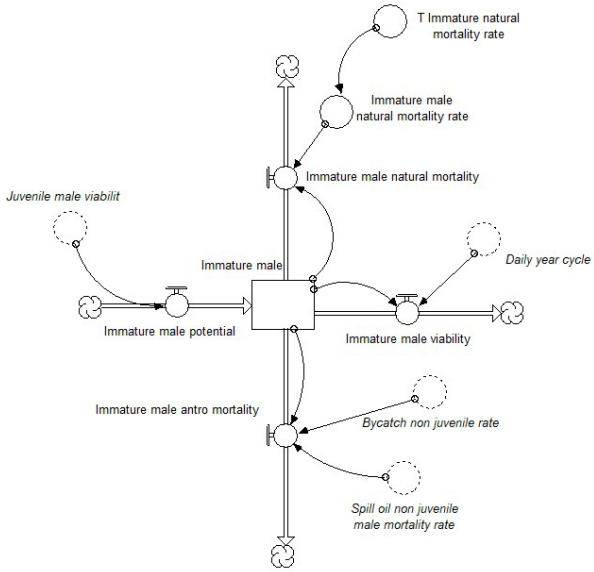


Figure S3. Stella software conceptual diagram of the sub-model of Immature male dynamics. Rectangles represent the state variables: Immature male; other variables, parameters or constants are small circles; sinks and sources are cloudlike symbols; flows are thick arrows; all the relations between state variables and other variables are fine arrows. The specification of all variable codes is expressed in Appendix II and main description in Table 1 of the manuscript.

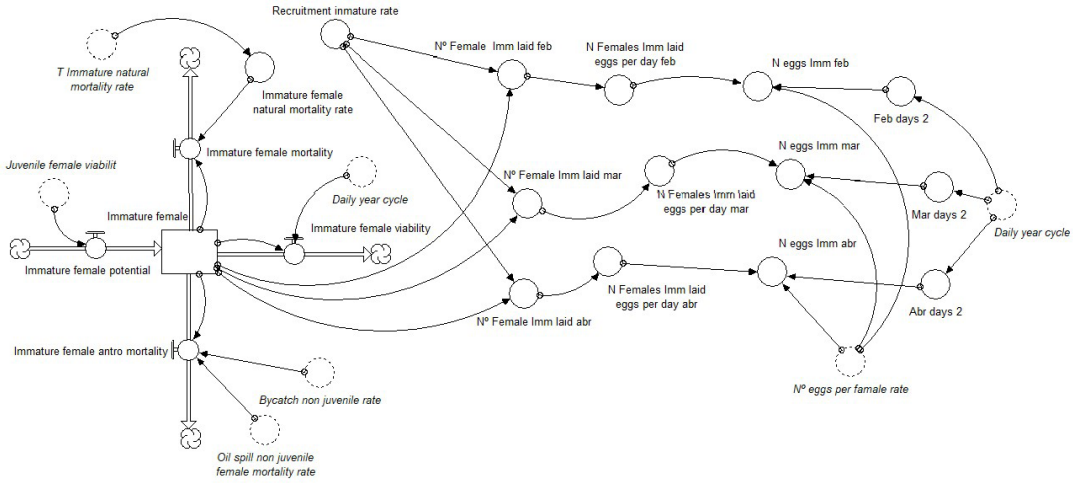


Figure S4. Stella software conceptual diagram of the sub-model of Immature female and breeding dynamics. Rectangles represent the state variables: Immature female; other variables, parameters or constants are small circles; sinks and sources are cloudlike symbols; flows are thick arrows; all the relations between state variables and other variables are fine arrows. The specification of all variable codes is expressed in Appendix II and main description in Table 1 of the manuscript.

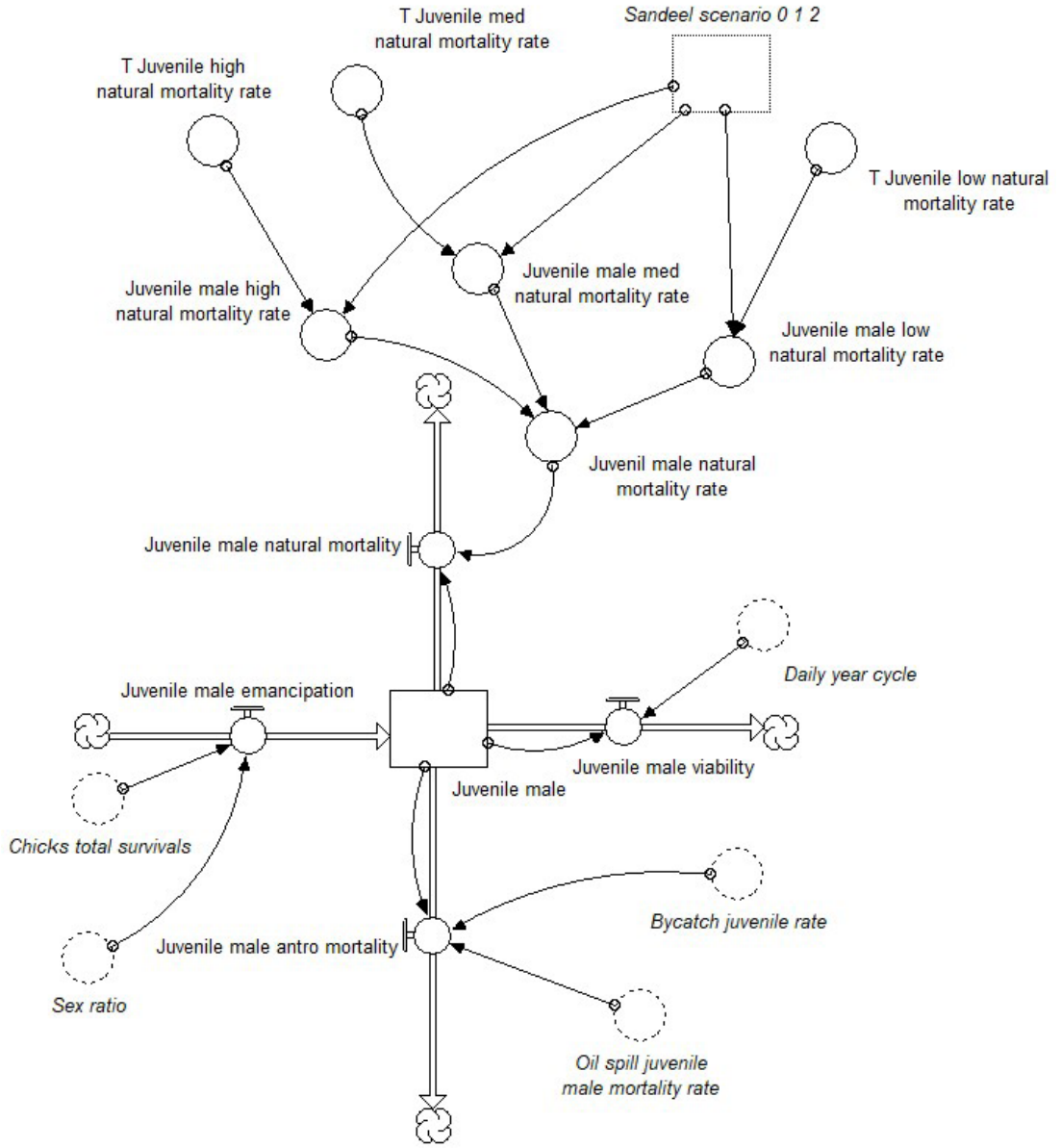


Figure S5. Stella software conceptual diagram of the sub-model of Juvenile male dynamics. Rectangles represent the state variables: Sandeels scenarios and Juvenile male; other variables, parameters or constants are small circles; sinks and sources are cloudlike symbols; flows are thick arrows; all the relations between state variables and other variables are fine arrows. The specification of all variable codes is expressed in Appendix II and main description in Table 1 of the manuscript.

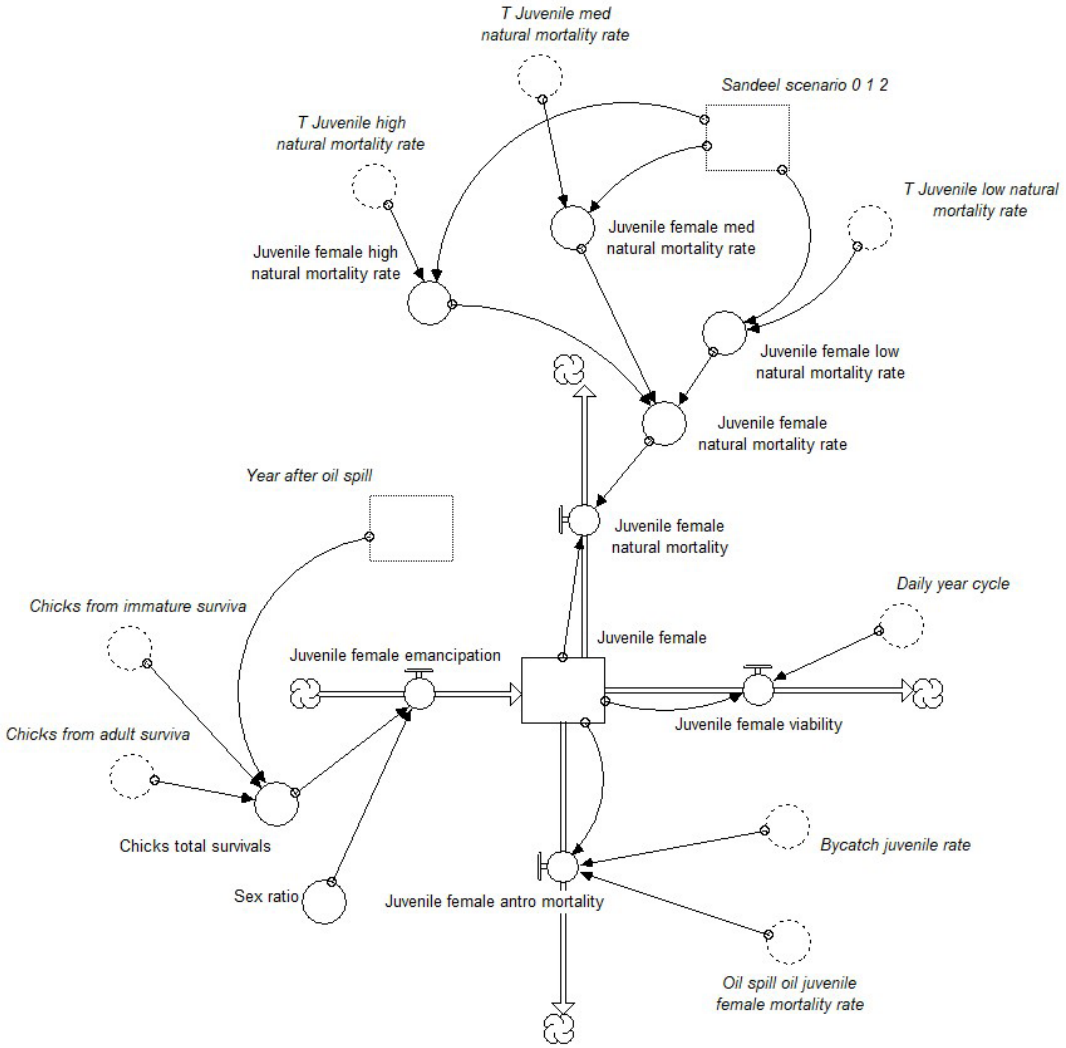


Figure S6. Stella software conceptual diagram of the sub-model of Juvenile female dynamics. Rectangles represent the state variables: Sandeels scenarios, Year after spill oil mortality and Juvenile female; other variables, parameters or constants are small circles; sinks and sources are cloudlike symbols; flows are thick arrows; all the relations between state variables and other variables are fine arrows. The specification of all variable codes is expressed in Appendix II and main description in Table 1 of the manuscript.

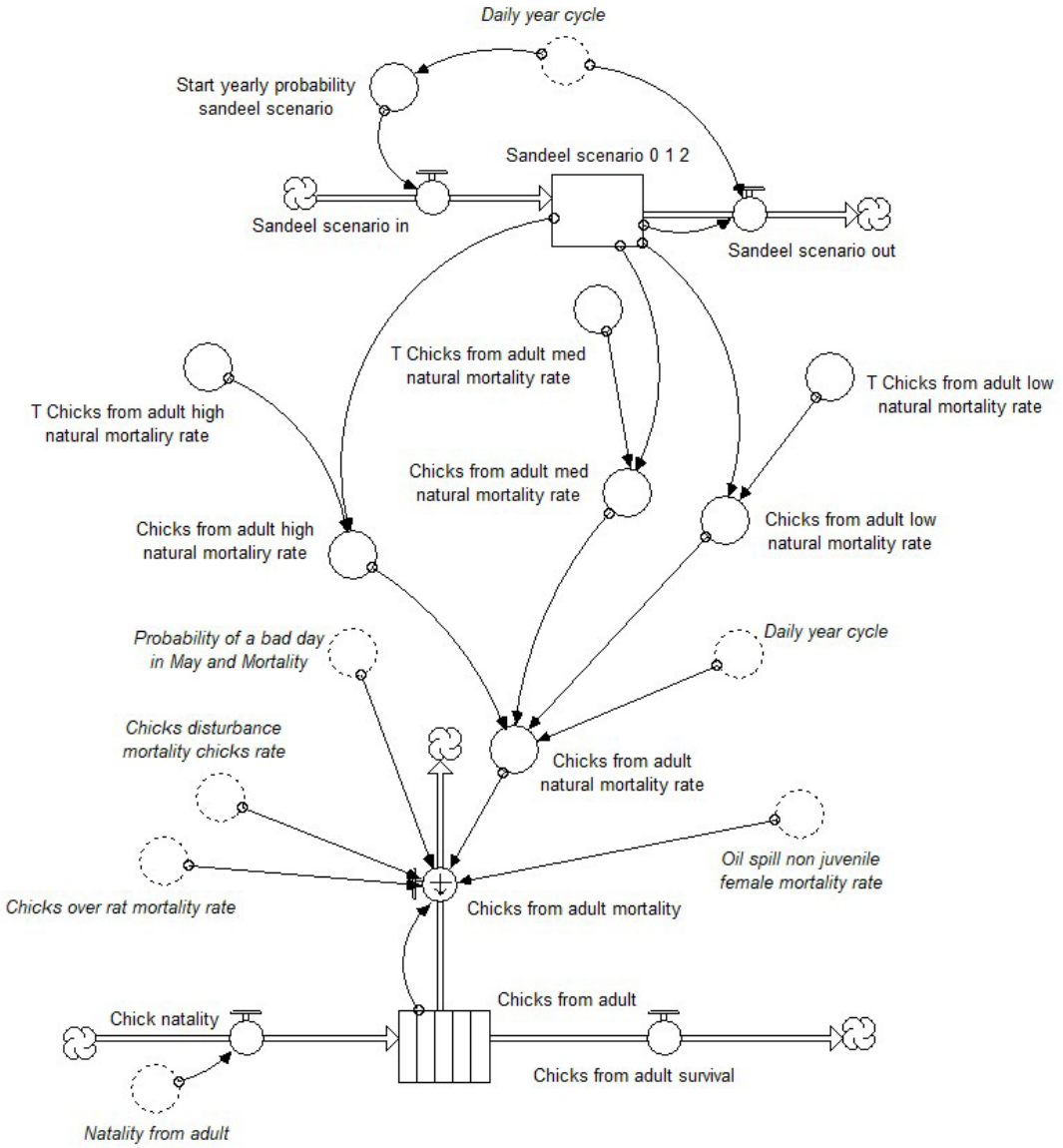


Figure S7. Stella software conceptual diagram of the sub-model of Chicks from adult dynamics. Rectangles represent the state variables: Sandeels scenarios and Chicks from adult; other variables, parameters or constants are small circles; sinks and sources are cloudlike symbols; flows are thick arrows; all the relations between state variables and other variables are fine arrows. The specification of all variable codes is expressed in Appendix II and main description in Table 1 of the manuscript.

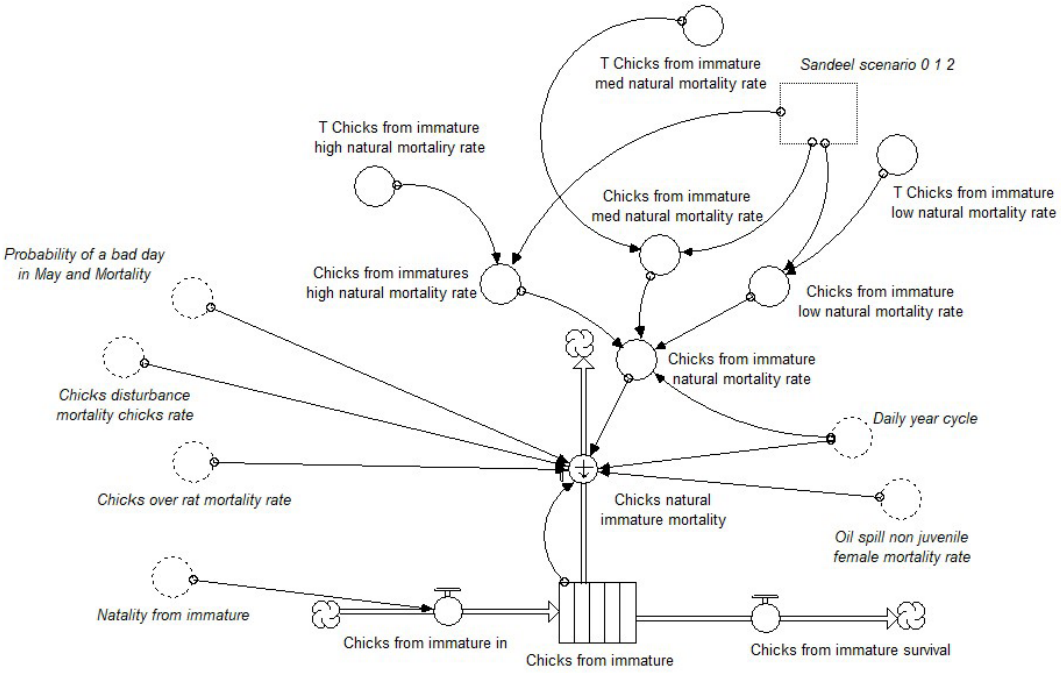


Figure S8. Stella software conceptual diagram of the sub-model of Chicks from immature dynamics. Rectangles represent the state variables: Sandeels scenarios and Chicks from immature; other variables, parameters or constants are small circles; sinks and sources are cloudlike symbols; flows are thick arrows; all the relations between state variables and other variables are fine arrows. The specification of all variable codes is expressed in Appendix II and main description in Table 1 of the manuscript.

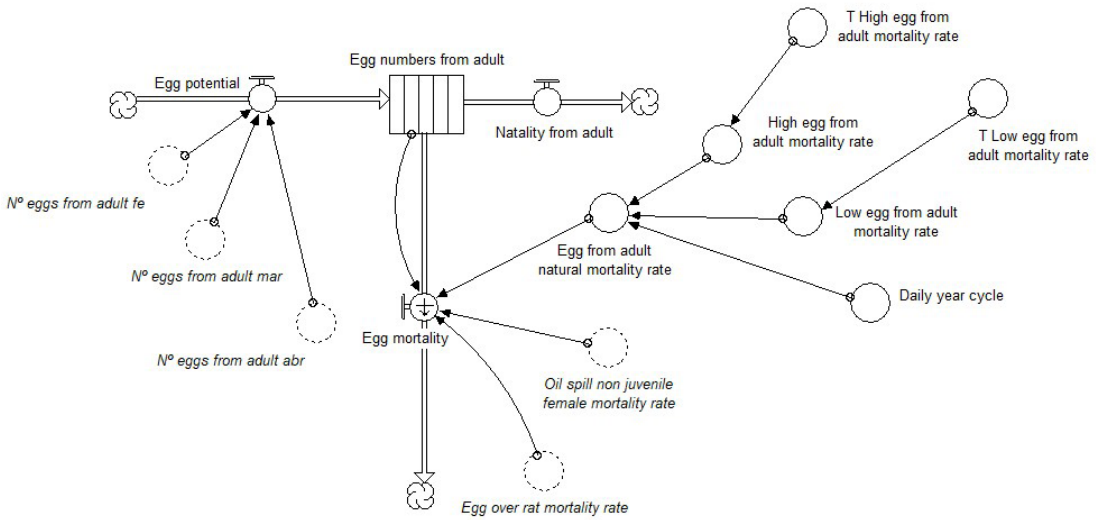


Figure S9. Stella software conceptual diagram of the sub-model of Eggs from adult dynamics. Rectangles represent the state variables: Eggs from adult; other variables, parameters or constants are small circles; sinks and sources are cloudlike symbols; flows are thick arrows; all the relations between state variables and other variables are fine arrows. The specification of all variable codes is expressed in Appendix II and main description in Table 1 of the manuscript.

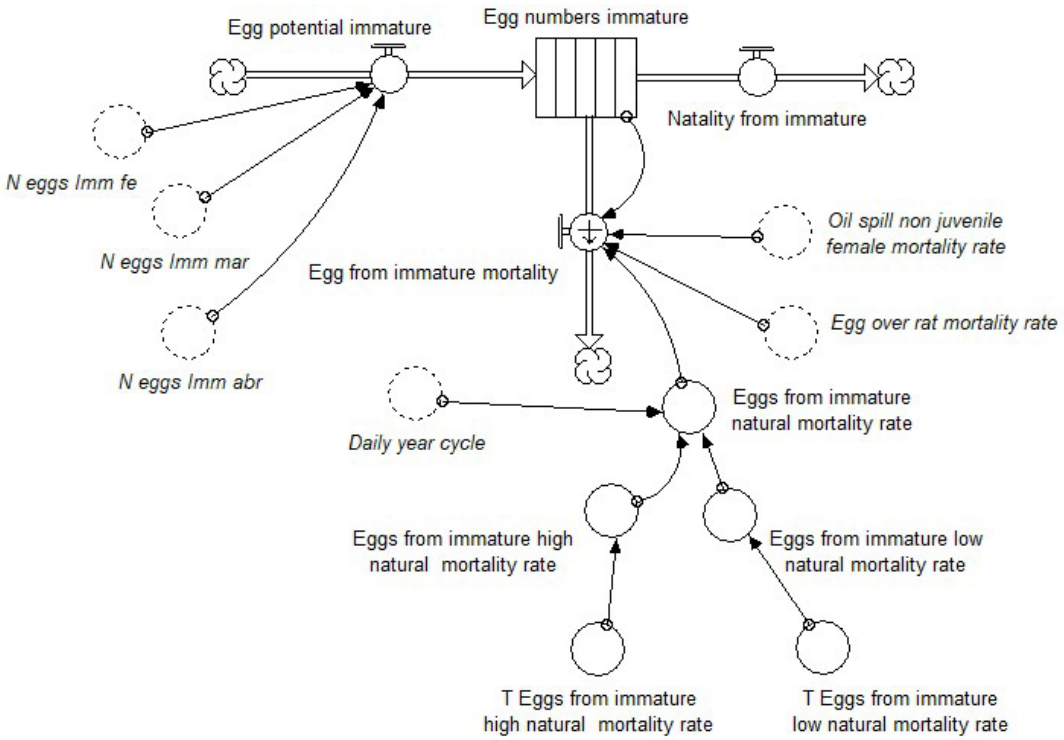


Figure S10. Stella software conceptual diagram of the sub-model of Eggs from immature dynamics. Rectangles represent the state variables: Sandeels scenarios, Eggs from immature and Chicks from immatures; other variables, parameters or constants are small circles; sinks and sources are cloudlike symbols; flows are thick arrows; all the relations between state variables and other variables are fine arrows. The specification of all variable codes is expressed in Appendix II and main description in Table 1 of the manuscript.

Key-factor sub-models

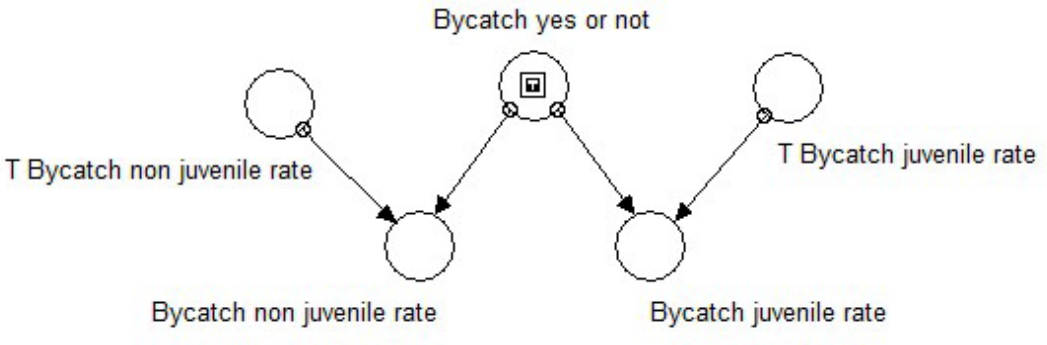


Figure S11. Stella software conceptual diagram of the sub-model of Bycatch dynamics. Small circles are variables, parameters or constants; all the relations between variables are fine arrows. The specification of all variable codes is expressed in Appendix II and main description in Table 1 of the manuscript.

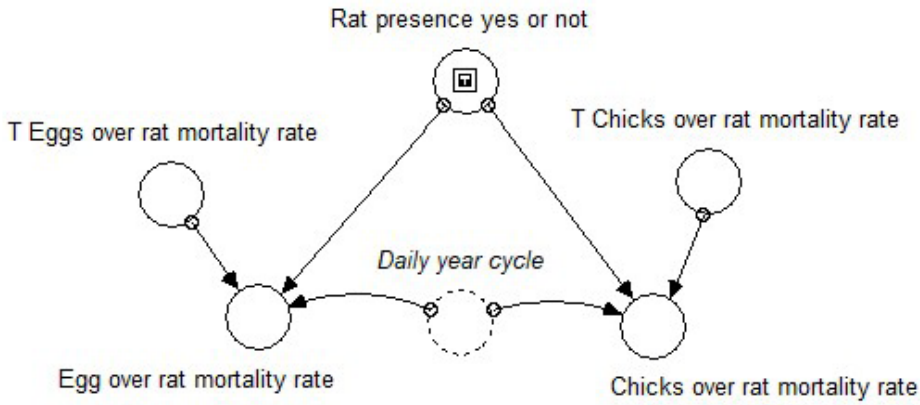


Figure S12 Stella software conceptual diagram of the sub-model of Mortality by Rat dynamics. Small circles are variables, parameters or constants; all the relations between variables are fine arrows. The specification of all variable codes is expressed in Appendix II and main description in Table 1 of the manuscript.

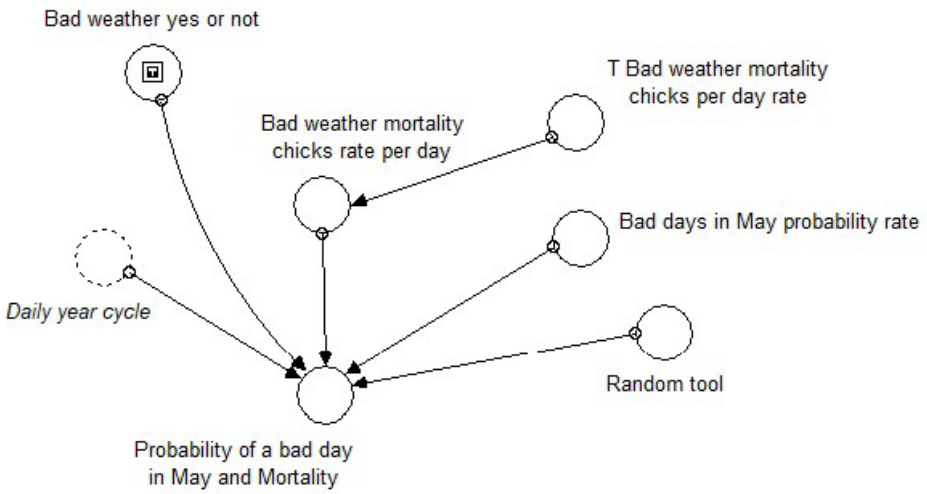


Figure S13. Stella software conceptual diagram of the sub-model of Bad weather mortality dynamics. Small circles are variables, parameters or constants; all the relations between variables are fine arrows. The specification of all variable codes is expressed in Appendix II and main description in Table 1 of the manuscript.

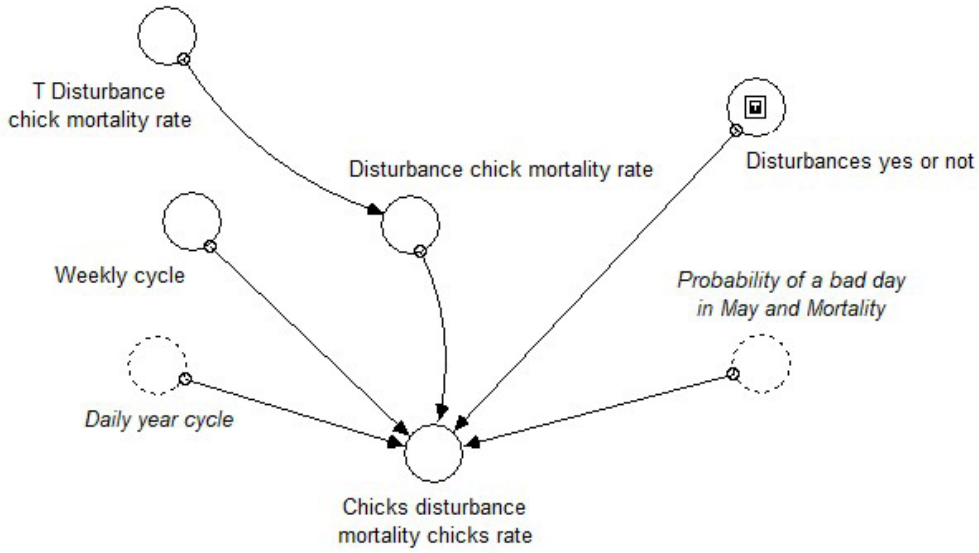


Figure S14. Stella software conceptual diagram of the sub-model of Tourism disturbance dynamics. Small circles are variables, parameters or constants; all the relations between variables are fine arrows. The specification of all variable codes is expressed in Appendix II and main description in Table 1 of the manuscript.

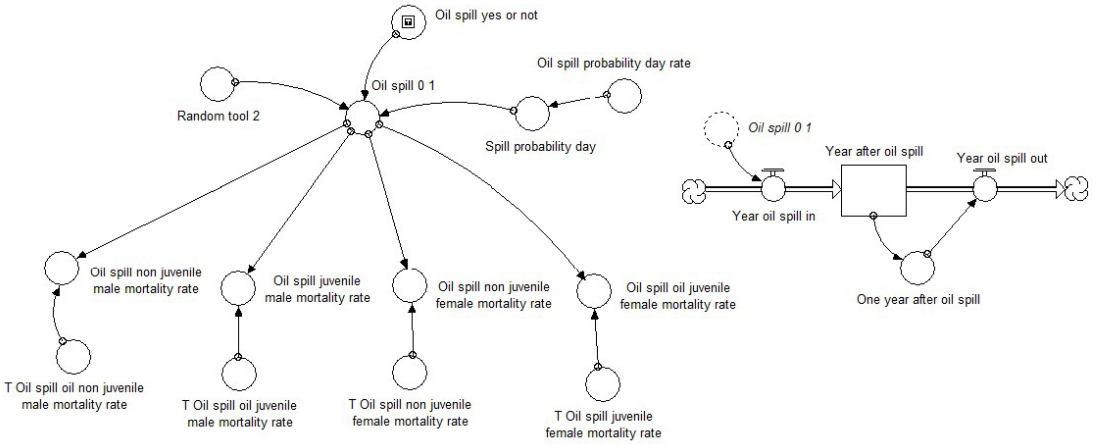


Figure S15. Stella software conceptual diagram of the sub-model of Oil spill catastrophe dynamics. Small circles are variables, parameters or constants; all the relations between variables are fine arrows. The specification of all variable codes is expressed in Appendix II and main description in Table 1 of the manuscript.

Appendix II. Mathematical equations associated with the model used to predict Shag dynamics in the Berlengas SPA

Table S1. Development and specification of all equations included in the model. The description of the main variables is expressed in Table 1.

Difference equations

Shag population dynamics

Adults

Adult_males(t) = Adult_males(t - dt) + (Adult_male_potential + Ad_male_in - Adult_male_antro_mortality - Adult_male_natural_mortaltiy - Ad_male_out) * dt
Adult_females(t) = Adult_females(t - dt) + (Adult_female_potential + Ad_female_in - Adult_female_natural_mortallity - Adult_female_antro_mortality - Ad_female_out) * dt

Immatures

Inmature_males(t) = Inmature_males(t - dt) + (Inmatures_male_potential + Imm_male_in - Inmatures_males_viability - Inmatures_male_antro_mortality - Inmatures_male_natural_mortality - Imm_male_out) * dt
Inmatures_female(t) = Inmatures_female(t - dt) + (Inmatures_female_potential + Imm_female_in - Inmatures_female_viability - Inmatures_female_mortality - Inmatures_female_antro_mortality - Imm_female_out) * dt

Juveniles

Juveniles_male(t) = Juveniles_male(t - dt) + (Juveniles_male_emancipation + Juv_male_in - Juveniles_male_viability - Juveniles_male_antro_mortality - Juveniles_male_natural_mortality - Juve_male_out) * dt
Juveniles_female(t) = Juveniles_female(t - dt) + (Juveniles_female_emancipation + Juve_female_in - Juveniles_female_viability - Juveniles_female_antro_mortality - Juveniles_female_natural_mortality - Juve_female_out) * dt

Chicks from adults

Chicks_from_adults(t) = Chicks_from_adults(t - dt) + (Chick_natality - Chicks_from_adults_survival - Chicks_from_adults_mortality) * dt

Chicks from immatures

Chicks_from_immatures(t) = Chicks_from_immatures(t - dt) + (Natality_from_inmatures - Chicks_from_

inmatures_survival - Chicks_natural_inmature_mortality) * dt

Eggs from adults

Egg_numbers_from_adults(t) = Egg_numbers_from_adults(t - dt) + (Egg_potential - Egg_mortality - Natality_from_adults) * dt

Eggs from immatures

Egg_numbers_inmatures(t) = Egg_numbers_inmatures(t - dt) + (Egg_potential_inmatures - Egg_from_immatures_mortality - Natality_from_inmatures) * dt

Others state variables

Female_breeders_percentage(t) = Female_breeders_percentaje(t - dt) + (Female_breeders_in - Female_breeders_out) * dt
Total_female_laid_eggs(t) = Total_female_laid_eggs(t - dt) + (Total_female_laid_eggs_in - Total_female_laid_eggs_out) * dt
Sandeel_scenario_0_1_2(t) = Sandeel_scenario_0_1_2(t - dt) + (Sandeel_scenario_in - Sandeel_scenario_out) * dt
Temperature_Feb(t) = Temperature_Feb(t - dt) + (Temp_Feb - Exit_Temp_Feb) * dt

Process equations

Shag population dynamics

Adult males

INIT Adult_male = 0
INFLOWS:
Adult_male_potential = Immature_male_viability
OUTFLOWS:
Adult_male_natural_mortaltiy = Adult_male*Adult_male_natural_mortality_rate
Adult_male_antro_mortality = Adult_male*Bycatch_non_juvenile_rate +
Adult_male*Oil_spill_non_juvenile_male_mortality_rate

Adult females and breeding dynamics

INIT Adult_females = 0
INFLOWS:
Adult_female_potential = Immature_female_viability
OUTFLOWS:

Adult_female_natural_mortallity = Adult_females*Adult_female_natural_mortality_rate
Adult_female_antro_mortality = Bycatch_non_juvenile_rate*Adult_females +
Adult_females*Oil_spill__non_juvenile_female_mortality_rate
INIT Female_breeders_percentaje = 0
INFLOWS:
Female_breeders_in = IF Daily_year_cycle = 2 THEN Correlation_female_vs_temp_Feb ELSE 0
OUTFLOWS:
Female_breeders_out = IF Daily_year_cycle =1 THEN Female_breeders_percentaje ELSE 0
INIT Temperature_Feb = 0
INFLOWS:
Temp_Feb = IF Daily_year_cycle = 1 THEN Random_Temp_Feb ELSE 0
OUTFLOWS:
Exit_Temp_Feb = IF Daily_year_cycle = 365 THEN Temperature_Feb ELSE 0

INIT Total_female_laid_eggs = 0
INFLOWS:
Total_female_laid_eggs_in = IF Feb_days = 1 THEN Nº_Adults_female_laid_eggs_per_day_feb + N_Females_Imm_laid_eggs_per_day_feb ELSE
(IF Mar_days = 1 THEN Nº_Adults_females_laid_eggs_per_day_mar + N_Females_Imm_laid_eggs_per_day_mar ELSE
(IF Abr_days =1 THEN Nº_Adults_females_laid_eggs_per_day_abr +N_Females_Imm_laid_eggs_per_day_abr ELSE 0))
OUTFLOWS:
Total_female_laid_eggs_out = IF Daily_year_cycle = 364 THEN Total_female_laid_eggs ELSE 0

Immature males

INIT Immature_male = 0
INFLOWS:
Immature_male_potential = Juvenile_male_viability
OUTFLOWS:
Immature_male_viability = IF Daily_year_cycle =30 THEN Immature_male ELSE 0
Immature_male_antro_mortality = Immature_male*Bycatch_non_juvenile_rate +
Immature_male*Oil_spill_non_juvenile_male_mortality_rate
Immature_male_natural_mortality = Immature_male*Immature_male_natural_mortality_rate

Immature females and breeding dynamics

INIT Immature_female = 0
INFLOWS:
Immature_female_potential = Juvenile_female_viability
OUTFLOWS:

Immature_female_viability = IF Daily_year_cycle =30 THEN Immature_female ELSE 0
Immature_female_mortality = Immature_female*Immature_female_natural_mortality_rate
Immature_female_antro_mortality = Immature_female*Bycatch_non_juvenile_rate +
Immature_female*Oil_spill_non_juvenile_female_mortality_rate

Juvenile males

INIT Juvenile_male = 0
INFLOWS:
Juvenile_male_emancipation = (1-Sex_ratio)*Chicks_total_survivals
OUTFLOWS:
Juvenile_male_viability = IF Daily_year_cycle =30 THEN Juvenile_male ELSE 0
Juvenile_male_natural_mortality = Juvenile_male*Juvenil_male_natural_mortality_rate
Juvenile_male_antro_mortality = Juvenile_male*Bycatch_juvenile_rate +
Juvenile_male*Oil_spill_juvenile_male_mortality_rate

Juvenile females

INIT Juvenile_female = 0
INFLOWS:
Juvenile_female_emancipation = Chicks_total_survivals*Sex_ratio
OUTFLOWS:
Juvenile_female_viability = IF Daily_year_cycle =30 THEN Juvenile_female ELSE 0
Juvenile_female_antro_mortality = Juvenile_female*Bycatch_juvenile_rate +
Juvenile_female*Oil_spill_juvenile_female_mortality_rate
Juvenile_female_natural_mortality = Juvenile_female*Juvenile_female_natural_mortality_rate

Chicks from adults

INIT Chicks_from_adult = 0
TRANSIT TIME = 55
INFLOW LIMIT = INF
CAPACITY = INF
INFLOWS:
Chick_natality = ROUND(Natality_from_adult)
OUTFLOWS:
Chicks_from_adult_survival = CONVEYOR OUTFLOW
Chicks_from_adult_mortality = LEAKAGE OUTFLOW
LEAKAGE FRACTION = (Probability_of_a_bad_day_in_May_and_Mortality+Chicks_from_adult_natural_mortality_rate+Chicks_over_rat_mortality_rate+Chicks_disturbance_mortality_chicks_rate+Oil_spill_non_juvenile_female_mortality_rate)*Chicks_from_adult
NO-LEAK ZONE = 0
INIT Sandeel_scenario_0_1_2 = 0

INFLOWS:
Sandeel_scenario_in = Start_yearly_probability_sandeel_scenario
OUTFLOWS:
Sandeel_scenario_out = IF Daily_year_cycle =365 THEN Sandeel_scenario_0_1_2 ELSE 0

Chicks from immatures

INIT Chicks_from_immature = 0
TRANSIT TIME = 55
INFLOW LIMIT = INF
CAPACITY = INF
INFLOWS:
Chicks_from_immature_in = Natality_from_immature
OUTFLOWS:
Chicks_from_immature_survival = CONVEYOR OUTFLOW
Chicks_natural_immature_mortality = LEAKAGE OUTFLOW
LEAKAGE FRACTION = IF Daily_year_cycle > 59 AND Daily_year_cycle < 213 THEN
(Probability_of_a_bad_day_in_May_and_Mortality+Chicks_from_immature_natural_mortality_rate+-
Chicks_over_rat_mortality_rate+Chicks_disturbance_mortality_chicks_rate+Oil_spill_non_juvenile_female_mortality_rate)*Chicks_from_immature ELSE 0
NO-LEAK ZONE = 0

Eggs from adults

INIT Egg_numbers_from_adult = 0
TRANSIT TIME = 30
INFLOW LIMIT = INF
CAPACITY = INF
INFLOWS:
Egg_potential = ROUND(Nº_eggs_from_adult_feb+Nº_eggs_from_adult_mar+Nº_eggs_from_adult_abr)
OUTFLOWS:
Egg_mortality = LEAKAGE OUTFLOW
LEAKAGE FRACTION = Egg_numbers_from_adult*Egg_from_adult_natural_mortality_rate +
Egg_numbers_from_adult*Egg_over_rat_mortality_rate +
Egg_numbers_from_adult*Oil_spill_non_juvenile_female_mortality_rate
NO-LEAK ZONE = 0
Natality_from_adult = CONVEYOR OUTFLOW

Eggs from immatures

INIT Egg_numbers_immature = 0
TRANSIT TIME = 30

INFLOW LIMIT = INF
CAPACITY = INF
INFLOWS:
Egg_potential_immature = N_eggs_Imm_feb+N_eggs_Imm_mar+N_eggs_Imm_abr
OUTFLOWS:
Egg_from_immature_mortality = LEAKAGE OUTFLOW
LEAKAGE FRACTION = Egg_numbers_immature*Egg_over_rat_mortality_rate +
Egg_numbers_immature*Oil_spill_non_juvenile_female_mortality_rate+
Egg_numbers_immature*Eggs_from_immature_natural_mortality_rate
NO-LEAK ZONE = 0
Natality_from_immature = CONVEYOR OUTFLOW

Composed variables

Shag population dynamics

Adult females and breeding dynamics

Feb_days = IF Daily_year_cycle > 31 AND Daily_year_cycle < 60 THEN 1 ELSE 0
Mar_days = IF Daily_year_cycle > 59 AND Daily_year_cycle < 91 THEN 1 ELSE 0
Apr_days = IF Daily_year_cycle > 90 AND Daily_year_cycle < 121 THEN 1 ELSE 0
Correlation_female_vs_temp_Feb = -0.1251*Temperature_Feb + 2.3746
Female_breeders_yearly = Female_breeders_percentaje*Adult_females
Max_Temp_Feb = if Daily_year_cycle = 1 then (15+ 0.000006 *TIME) ELSE 0
Min_Temp_Feb = if Daily_year_cycle = 1 then (12+ 0.000006 *TIME) ELSE 0
N°_Adults_female_laid_eggs_per_day_feb = N°_Adults_female_laid_feb/30
N°_Adults_females_laid_eggs_per_day_mar = N°_Adults_female_laid_mar/30
N°_Adults_females_laid_eggs_per_day_apr = N°_Adults_female_laid_apr/30
N°_Adults_female_laid_feb = (Adult_females*0.20)*Female_breeders_percentaje
N°_Adults_female_laid_mar = (Adult_females*0.60)*Female_breeders_percentaje
N°_eggs_from_adult_feb = Feb_days*N°_Adults_female_laid_eggs_per_day_feb*N°_eggs_per_famale_rate
N°_eggs_from_adult_mar = Mar_days*N°_eggs_per_famale_rate*N°_Adults_females_laid_eggs_per_day_mar
N°_eggs_from_adult_apr = Apr_days*N°_eggs_per_famale_rate*N°_Adults_females_laid_eggs_per_day_apr
N°_Adults_female_laid_apr = (Adult_females*0.20)*Female_breeders_percentaje

Immature females and breeding dynamics

Feb_days_2 = IF Daily_year_cycle > 31 AND Daily_year_cycle < 60 THEN 1 ELSE 0
Apr_days_2 = IF Daily_year_cycle > 90 AND Daily_year_cycle < 121 THEN 1 ELSE 0

Mar_days_2 = IF Daily_year_cycle > 59 AND Daily_year_cycle < 91 THEN 1 ELSE 0
N_eggs_Imm_feb = Feb_days_2*N_Females_Imm_laid_eggs_per_day_feb*N°_eggs_per_famale_rate
N_eggs_Imm_mar = Mar_days_2*N°_eggs_per_famale_rate*N_Females_Imm_laid_eggs_per_day_mar
N_eggs_Imm_apr = Apr_days_2*N°_eggs_per_famale_rate*N_Females_Imm_laid_eggs_per_day_apr
N_Females_Imm_laid_eggs_per_day_feb = N°_Female__Imm_laid_feb/30
N_Females_Imm_laid_eggs_per_day_mar = N°_Female_Imm_laid_mar/30
N_Females_Imm_laid_eggs_per_day_apr = N°_Female_Imm_laid_apr/30
N°_Female_Imm_laid_feb = ROUND(Immature_female*Recruitment_inmature_rate*0.20)
N°_Female_Imm_laid_mar = ROUND(Immature_female*Recruitment_inmature_rate*0.60)
N°_Female_Imm_laid_apr = ROUND(Immature_female*Recruitment_inmature_rate*0.20)

Juvenile males

Juvenile_male_low_natural_mortality_rate = IF Sandeel_scenario_0_1_2 = 2 THEN
NORMAL(T_Juvenile_low_natural_mortality_rate,0.00005) ELSE 0
Juvenile_male_med_natural_mortality_rate = IF Sandeel_scenario_0_1_2 =1 THEN
NORMAL(T_Juvenile_med_natural_mortality_rate,0.0005) ELSE 0
Juvenile_male_high_natural_mortality_rate = IF Sandeel_scenario_0_1_2 = 0 THEN
NORMAL(T_Juvenile_high_natural_mortality_rate,0.0005) ELSE 0
Juvenil_male_natural_mortality_rate = (Juvenile_male_high_natural_mortality_rate+
Juvenile_male_low_natural_mortality_rate + Juvenile_male_med_natural_mortality_rate)

Juvenile females

Chicks_total_survivals = IF Year_after_oil_spill =1 THEN 0.5*(Chicks_from_adult_survival+Chicks_from_immature_survival) ELSE (Chicks_from_adult_survival+Chicks_from_immature_survival)
Juvenile_female_low_natural_mortality_rate = IF Sandeel_scenario_0_1_2 = 2 THEN
NORMAL(T_Juvenile_low_natural_mortality_rate,0.00005) ELSE 0
Juvenile_female_med_natural_mortality_rate = IF Sandeel_scenario_0_1_2 =1 THEN
NORMAL(T_Juvenile_med_natural_mortality_rate,0.0005) ELSE 0
Juvenile_female_high_natural_mortality_rate = IF Sandeel_scenario_0_1_2 = 0 THEN
NORMAL(T_Juvenile_high_natural_mortality_rate,0.0005) ELSE 0
Juvenile_female_natural_mortality_rate = (Juvenile_female_high_natural_mortality_rate+
Juvenile_female_low_natural_mortality_rate + Juvenile_female_med_natural_mortality_rate)

Chicks from adults

Chicks_from_adult_low_natural_mortality_rate = IF Sandeel_scenario_0_1_2 = 2 THEN
NORMAL(T_Chicks_from_adult_low_natural_mortality_rate,0.0005) ELSE 0
Chicks_from_adult_med_natural_mortality_rate = IF Sandeel_scenario_0_1_2 =1 THEN
NORMAL(T_Chicks_from_adult_med_natural_mortality_rate,0.0005) ELSE 0
Chicks_from_adult_high_natural_mortaliry_rate = IF Sandeel_scenario_0_1_2 = 0 THEN
NORMAL(T_Chicks_from_adult_high_natural_mortaliry_rate,0.0005) ELSE 0

Chicks_from_adult_natural_mortality_rate = (IF Daily_year_cycle >59 AND Daily_year_cycle <213 THEN
(Chicks_from_adult_high_natural_mortaliry_rate +
Chicks_from_adult_low_natural_mortality_rate +
Chicks_from_adult_med_natural_mortality_rate) ELSE 0)
Start_yearly_probability_sandeel_scenario = IF Daily_year_cycle =1 THEN ROUND(RANDOM(0,2)) ELSE 0

Chicks from immatures

Chicks_from_immature_low_natural_mortality_rate = IF Sandeel_scenario_0_1_2 = 2 THEN NORMAL(T_Chicks_from_immature_low_natural_mortality_rate,0.0005) ELSE 0
Chicks_from_immature_med_natural_mortality_rate = IF Sandeel_scenario_0_1_2 = 1 THEN NORMAL(T_Chicks_from_immature_med_natural_mortality_rate,0.0005) ELSE 0
Chicks_from_immatures_high_natural_mortality_rate = IF Sandeel_scenario_0_1_2 = 0 THEN NORMAL(T_Chicks_from_immature_high_natural_mortaliry_rate,0.0005) ELSE 0
Chicks_from_immature_natural_mortality_rate = (IF Daily_year_cycle >59 AND Daily_year_cycle <213 THEN (Chicks_from_immatures_high_natural_mortality_rate + Chicks_from_immature_low_natural_mortality_rate + Chicks_from_immature_med_natural_mortality_rate) ELSE 0)

Eggs from adults

Egg_from_adult_natural_mortality_rate = (IF Daily_year_cycle > 31 AND Daily_year_cycle < 121 THEN RANDOM(Low_egg_from_adult_mortality_rate,High_egg_from_adult_mortality_rate) ELSE 0)

Eggs from immatures

Eggs_from_immature_natural_mortality_rate = (IF Daily_year_cycle > 31 AND Daily_year_cycle < 121 THEN RANDOM(Eggs_from_immature_low_natural_mortality_rate, Eggs_from_immature_high_natural_mortality_rate) ELSE 0)

Composed variables

Anthropogenic and Ecological factors

Bycatch mortality

Bycatch_juvenile_rate = IF Bycatch_yes_or_not = 1 THEN NORMAL(T_Bycatch_juvenile_rate,0.00005) ELSE 0
Bycatch_non_juvenile_rate = IF Bycatch_yes_or_not = 1 THEN

NORMAL (T_Bycatch_non_juvenile_rate,0.000005) ELSE 0
Bycatch_yes_or_not = 0

Mortality due to rats

Chicks_over_rat_mortality_rate = IF Rat_presence_yes_or_not = 1 AND Daily_year_cycle > 59 AND Daily_year_cycle < 213 THEN RANDOM (0,T_Chicks_over_rat_mortality_rate) ELSE 0
Egg_over_rat_mortality_rate = IF Daily_year_cycle > 31 AND Daily_year_cycle < 121 AND Rat_presence_yes_or_not = 1 THEN RANDOM (0,T_Eggs_over_rat_mortality_rate) ELSE 0
Rat_presence_yes_or_not = 0

Adverse weather and chick mortality

Bad_days_in_May_probability_rate = 0.019
Bad_weather_yes_or_not = 1
Probability_of_a_bad_day_in_May_and_Mortality = IF Bad_weather_yes_or_not =1 THEN
(IF Daily_year_cycle > 120 AND Daily_year_cycle < 152 THEN
(IF Random_tool < Bad_days_in_May_probability_rate THEN
Bad_weather_mortality_chicks_rate_per_day ELSE 0) ELSE 0) ELSE 0

Tourism disturbance-associated mortality

Chicks_disturbance_mortality_chicks_rate = IF Disturbances_yes_or_not =1 AND Probability_of_a_bad_day_in_May_and_Mortality = 0 THEN
(IF (Daily_year_cycle > 59 AND Daily_year_cycle < 213) AND
Weekly_cycle >5 THEN Disturbance_chick_mortality_rate ELSE 0) ELSE 0
Disturbances_yes_or_not = 1

Oil spill mortality

Year_after_oil_spill(t) = Year_after_oil_spill(t - dt) + (Year_oil_spill_in - Year_oil_ spill_out) * dt
INIT Year_after_oil_spill = 0
INFLOWS:
Year_oil_spill_in = IF Oil_spill_0_1 = 1 THEN 1 ELSE 0
OUTFLOWS:
Year_oil_spill_out = if One_year_after_oil spill = 365 THEN 1 ELSE 0
One_year_after_oil_spill = IF Year_after_oil spill = 1 THEN COUNTER (1,366) ELSE 0
Oil_spilloil_0_1 = if (Oil_spill_yes_or_not = 1) THEN
(IF Random_tool_2 < Spill_probability_day THEN 1 ELSE 0) ELSE 0
Oil_spill_juvenile_male_mortality_rate = IF Oil_spill_0_1 = 1 THEN
NORMAL(T_Oil_spill_juvenile_male_mortality_rate,0.0005) ELSE 0
Oil_spill_juvenile_female_mortality_rate = IF Oil_spill_0_1 = 1 THEN

NORMAL(T_Oil_spill_juvenile_female_mortality_rate,0.005) ELSE 0
Oil_spill_non_juvenile_male_mortality_rate = IF Oil_spill_0_1 = 1 THEN
NORMAL (T_Oil_spill_non_juvenile_male_mortality_rate,0.0005) ELSE 0
Oil spill_yes_or_not = 0
Oil spill__non_juvenile_female_mortality_rate = IF Oil_spill_0_1 = 1 THEN
NORMAL(T_Oil_spill_non_juvenile_female_mortality_rate,0.005) ELSE 0
Spill_probability_day = NORMAL(Oil_spill_probability_day_rate,0.00005)

Constants

T_Adult_natural_mortality_rate_min = 0.00045357
T_Adult_natural_mortality_rate_max = 0.00076092
T_Immature_natural_mortality_rate = 0.00071906
T_Juvenile_low_natural_mortality_rate = 0.00089627
T_Juvenile_med_natural_mortality_rate = 0.001271312
T_Juvenile_high_natural_mortality_rate = 0.00138064
T_Chicks_from_adult_low_natural_mortality_rate = 0.00234091
T_Chicks_from_adult_med_natural_mortality_rate = 0.00332044
T_Chicks_from_adult_high_natural_mortaliry_rate = 0.00360600
T_Chicks_from_immature_low_natural_mortality_rate = 0.00286610
T_Chicks_from_immature_med_natural_mortality_rate = 0.00406540
T_Chicks_from_immature_high_natural_mortaliry_rate = 0.00441502
T_Low_egg_from_adult_mortality_rate = 0.00719615
T_High_egg_from_adult_mortality_rate = 0.01079396
T_Eggs_from_immature_low_natural_mortality_rate = 0.01315383
T_Eggs_from_immature_high_natural_mortality_rate = 0.01579016
T_Bycatch_juvenile_rate = 0.000251925
T_Bycatch_non_juvenile_rate = 0.00008284
T_Chicks_over_rat_mortality_rate = 0.00623262
T_Eggs_over_rat_mortality_rate = 0.016667885
T_Bad_weather_mortality_chicks_per_day_rate = 0.00110566
T_Disturbance_chick_mortality_rate = 0.00110566
Oil_spill_probability_day_rate = 0.000304414
T_Oil_spill_juvenile_female_mortality_rate = 0.02805
T_Oil_spill_juvenile_male_mortality_rate = 0.00495
T_Oil_spill_non_juvenile_female_mortality_rate = 0.014025
T_Oil_spill_non_juvenile_male_mortality_rate = 0.002475

Random variables

Adult_male_natural_mortality_rate = RANDOM (T_Adult_natural_mortality_rate_min, T_Adult_natural_mortality_rate_max)
Adult_female_natural_mortality_rate = RANDOM (T_Adult_natural_mortality_rate_min,T_Adult_natural_mortality_rate_max)
Random_Temp_Feb = RANDOM(Min_Temp_Feb,Max_Temp_Feb)
Random_tool = RANDOM (0,1)
Random_tool_2 = RANDOM (0,1)
Sex_ratio = Random (0.49,0.51)
N°_eggs_per_famale_rate = POISSON (2.5)
Immature_male_natural_mortality_rate = NORMAL(T_Immature_natural_mortality_rate,0.00005)
Immature_female_natural_mortality_rate = NORMAL (T_Immature_natural_mortality_rate ,0.00005)
Recruitment_inmature_rate = NORMAL (0.47,0.05)
Eggs_from_immature_high_natural__mortality_rate = NORMAL(T_Eggs_from_immature_high_natural__mortality_rate,0.005)
Eggs_from_immature_low_natural_mortality_rate = NORMAL(T_Eggs_from_immature_low_natural_mortality_rate,0.005)
High_egg_from_adult_mortality_rate = NORMAL(T_High_egg_from_adult_mortality_rate,0.005)
Low_egg_from_adult_mortality_rate = NORMAL(T_Low_egg_from_adult_mortality_rate,0.00025)
Bad_weather_mortality_chicks_rate_per_day = NORMAL(T_Bad_weather_mortality_chicks_per_day_rate, 0.0005)
Disturbance_chick_mortality_rate = NORMAL (T_Disturbance_chick_mortality_rate,0.0005)

Other variables

Daily_year_cycle = counter (1,366)
Weekly_cycle = COUNTER (1,8)

Appendix III. Details and explanation of the dynamic model used to predict Shag population dynamics in the Berlengas SPA

- PURPOSE: The model intends to recreate the Berlengas' Shag population dynamics, considering current biological and ecological constrains, environmental conditions and their interplay with management actions. All the equations are depicted in Appendix II, table S1.

- STRUCTURE AND FUNCTIONING

1. **Shag population dynamics**
2. **Influence of anthropogenic and ecological factors**

1. SHAG POPULATION DYNAMICS

Shags breeding season in Berlengas runs from February to July. The laying season was defined between February and April. Eggs hatch after one month of incubation period, from March to May, depending on the month they were laid. After hatching, chicks fledge to juveniles after 55 days, from late April until mid-July (Cramp & Simmons, 1977; Neto, 1997; Silva, 2015).

Modelling elements:

- Adult laying season (*Feb_days*, *Mar_days*, *_Apr_days*) (Table S1. – 'Composed variables').
- Immature laying season (*Feb_days_2*, *Mar_days_2*, *Apr_days_2)* (Table S1. – 'Composed variables').
- Seasonality (*Daily_year_cycle*) (Table S1. – 'Other variables').

To reproduce and model the complete Shag life cycle, five life stages were considered: adults (more than two years old; males and females), immatures (more than one year old; males and females), juveniles (birds that fledged in late April to mid-July until next February; males and females), chicks (55 days in the nest during March to mid-July) and eggs (30 days of incubation stage from February to April). A total of 10 state variables were considered to represent the number of individuals in each demographic stage (Figs. S1-S10, Appendix I).

Since the model runs on a daily basis, as general rule, daily rates were calculated from % of annual/monthly rates following the equation 1:

Daily rate=[(1+R/100)^(1/d)]-1

Where R is the initial yearly/monthly rate and d is number of days included in R (Newnan, Eschenbach, & Lavelle, 2004). Instead of a single value, rates were associated to specific distributions, supported on data and or literature (e.g. minimum and maximum values) to increase the realism of simulations (Cressie *et al*., 2009; Johnson *et al*., 2014).

STATE VARIABLES

- **Adults** (*Adult males*, *Adult females*) (Table S1. – 'Difference equations').
- **Immatures** (*Immature males*, *Immature females*) (Table S1. – 'Difference equations').
- **Juveniles** (*Juvenile males*, *Juvenile females*) (Table S1. – 'Difference equations').
- **Chicks from adults** (*Chicks from adults*) (Table S1. – 'Difference equations').
- **Chicks from immatures** (*Chicks from immatures*) (Table S1. – 'Difference equations').
- **Eggs from adults** (*Eggs numbers adults*) (Table S1. – 'Difference equations').
- **Eggs from immatures** (*Eggs numbers immatures*) (Table S1. – 'Difference equations').

1.1 Adults

The dynamics of breeding adult result from the balance between immatures that reach to adulthood and total mortality. Adult birds are assumed to be ≥ 3 years old and can breed every year. New breeding adults (coming from immatures) enter into the reproductive population with a sex ratio 1:1 (Snow, 1960; Velando & Freire, 2002). The initial number of adult birds was assumed as 164 birds (82 males and 82 females) according to the maximum number of breeding birds recorded during annual censuses from the last decade (Pereira & Oliveira, 2019).

Modelling elements:

Adult_male_potential (Table S1. – 'Process equations').

Adult_female_potential (Table S1. – 'Process equations').

Adult natural mortality

Literature values point to annual mortality rates between 0.18 and 0.32 (Velando & Freire, 2002). These values were transformed to daily rates (min: 0.00045 and max: 0.00076)

and applied into the model following a random distribution.

Modelling elements:

Adult_male_natural_mortaltiy (Table S1. – 'Process equations').

Adult_female_natural_mortaltiy (Table S1. – 'Process equations').

Adult_male_natural_mortality_rate (Table S1. – 'Random variables').

Adult_female_natural_mortality_rate (Table S1. – 'Random variables').

T_Adult_natural_mortality_rate_min (Table S1. – 'Constant').

T_Adult_natural_mortality_rate_max (Table S1. – 'Constant').

Breeding potential according to winter sea surface temperature

Seabirds have been declining worldwide and environmental variability is believed to be one of the main causes driving such trend (Daunt and Mitchell, 2013). In this perspective, sea temperatures, namely during the winter, have been associated with a reduction in fish productivity that affects seabird fat reserves, reducing their reproductive success (Wright, Orpwood, & Scott, 2017). In order to estimate the influence of sea surface temperature (SST) in the potential number of breeding females at Berlengas, we related the number of breeding pairs registered in censuses from the last decade in Berlengas (Pereira & Oliveira, 2019) with meteorological data recorded in February of the same period at the Cabo Silleiro buoy (Ministry of Development, 2020). This relation followed the equation: $y= -0.1251x+2.3746$ ($R^2 = 0.1655$), where y is the number of breeding pairs and x is the SST in February. This enabled to set, in the model, the proportion of adult females breeding each year, considering random variations in SST during February (minimum= 12 °C and maximum= 15 °C; Ministerio de Fomento, 2020).

Modelling elements:

Correlation_female_vs_temp_Feb (Table S1. – 'Composed variables').

Female_breeders_yearly (Table S1. – 'Composed variables').

1.2 Immatures

Immatures result from the surviving juvenile birds that transit to the immature age class (2 years old) (Snow, 1960; Velando & Freire, 2002).

Modelling elements:

Immature_male_potential (Table S1. – 'Process equations').

Immature_female_potential (Table S1. – 'Process equations').

Immatures natural mortality

An immature average natural mortality rate of 0.30 individuals per year (Velando & Munilla, 2008) was transformed into daily natural mortality rate of 0.0007 individuals per day and applied in our model as a normal distribution with mean of the daily rate and SD of 0.1 of the average daily rate (Cressie *et al*., 2009).

Modelling elements:

Immature_male_natural_mortality_rate (Table S1. – 'Composed variables').

Immature_female_natural_mortality_rate (Table S1. – 'Composed variables').

T_Immature_natural_mortality_rate (Table S1. – 'Constant').

Potential of breeding according to winter sea surface temperature

To recreate the effect of sea water temperature on immature females' breeding potential, we used the same relation between SST and adult females to simulate the potential proportion of breeding immatures female that reproduce each year. Additionally, not all the immature birds breeds every year, so a 0.47 recruitment rate (Velando & Freire, 2002) was applied as a normal distribution with a SD of 0.1 of the average daily rate (Cressie *et al*., 2009) to complete the total number of immature females breeding per year.

Modelling elements:

Recruitment_inmature_rate (Table S1. – 'Composed variables').

1.3 Juveniles

uvenile birds result from the surviving chicks from both adult and immature birds, applying a sex ratio of 50% (random between 0.49-0.51) (Velando & Freire, 2002).

Modelling elements:

Chicks_total_survivals (Table S1. – 'Composed variables').

Juvenile_male_emancipation (Table S1. – 'Process equations').

Juvenile_female_emancipation (Table S1. – 'Process equations').

Sex ratio (Table S1. – 'Random variable').

Juvenile natural mortality

The natural juvenile mortality rate is partially related to sandeels availability (R. W. Furness, 2002). To consider this food fluctuation, we established three random scenarios with minimum, medium and maximum availability of sandeels (see below, anthropogenic and ecological factors), and consequently we calculated a reduction or increase in mortality rate using the rate described in Furness and Tasker (2000) (29% increase in productivity during years of high abundance of sandeels and an 8.6% decrease in years of scarce resources). After transform this mortality to daily rate, we applied a normal distribution of this variation rate based on sandeels availability to the juvenile average natural mortality rate described in Velando and Munilla (2011a).

Modelling elements:

Juvenil_male_natural_mortality_rate (Table S1. – 'Composed variables').

Juvenile_male_low_natural_mortality_rate (Table S1. – 'Composed variables').

Juvenile_male_med_natural_mortality_rate (Table S1. – 'Composed variables').

Juvenile_male_high_natural_mortality_rate (Table S1. – 'Composed variables').

Juvenil_female_natural_mortality_rate (Table S1. – 'Composed variables').

Juvenile_female_low_natural_mortality_rate (Table S1. – 'Composed variables').

Juvenile_female_med_natural_mortality_rate (Table S1. – 'Composed variables').

Juvenile_female_high_natural_mortality_rate (Table S1. – 'Composed variables').

T_Juvenile_low_natural_mortality_rate (Table S1. – 'Constant').

T_Juvenile_med_natural_mortality_rate (Table S1. – 'Constant').

T_Juvenile_high_natural_mortality_rate (Table S1. – 'Constant').

1.4 Chicks

Nestling birds. The dynamic of chicks results from the balance between eggs hatched from eggs laid by adults and by immatures birds. The chick-rearing period lasts 55 days, and nestlings become juveniles after fledging. The initial number of chicks was considered 0 since the beginning of the simulation (January) does not correspond to the breeding season.

Modelling elements:

Chicks_from_adult (Table S1. – 'Process equations).

Chicks_from_immature (Table S1. – 'Process equations).

Chicks natural mortality

Like for juveniles, natural chicks mortality rate is related to sandeels availability, so we applied the same three random scenarios of sandeels abundance and consequently we repeat the same calculus of reduction or increase in mortality rate using the rate described in Furness and Tasker (2000). In the same way, after transformed to daily rates, we applied a normal distribution of this variation rate based on sandeels availability to the chicks average natural mortality rate described in Velando and Freire (2002).

Modelling elements:

Chicks_from_adult_natural_mortality_rate (Table S1. – 'Composed variables').

Chicks_from_immature_natural_mortality_rate (Table S1. – 'Composed variables').

Chicks_from_adult_low_natural_mortality_rate (Table S1. – 'Composed variables).

Chicks_from_adult_med_natural_mortality_rate (Table S1. – 'Composed variables).

Chicks_from_adult_high_natural_mortaliry_rate (Table S1. – 'Composed variables).

Chicks_from_immatures_high_natural_mortality_rate (Table S1. – 'Composed variables).

Chicks_from_immature_low_natural_mortality_rate (Table S1. – 'Composed variables).

Chicks_from_immature_med_natural_mortality_rate (Table S1. – 'Composed variables).

T_Chicks_from_adult_low_natural_mortality_rate (Table S1. – 'Constant').

T_Chicks_from_adult_med_natural_mortality_rate (Table S1. – 'Constant').

T_Chicks_from_adult_high_natural_mortaliry_rate (Table S1. – 'Constant').

T_Chicks_from_immature_low_natural_mortality_rate (Table S1. – 'Constant').

T_Chicks_from_immature_med_natural_mortality_rate (Table S1. – 'Constant').

T_Chicks_from_immature_high_natural_mortaliry_rate (Table S1. – 'Constant').

1.5 Eggs

Eggs laid by females (adults and immatures) are incubated for one month. The clutch size results from the number of eggs laid from adult females and immature females breeding (Snow, 1960; Velando & Freire, 2002). The initial number of eggs was considered 0, since the beginning of the simulation (January) does not correspond to the breeding season.

Modelling elements:

Egg_numbers_from_adult (Table S1. – 'Process equations).

Egg_numbers_immature (Table S1. – 'Process equations).

Eggs laying

The egg-laying period extends from February to April. Since the highest egg-laying rates are in March (Neto, 1997; Silva, 2015), we assumed different laying intensities throughout the egg laying season, namely 0.20 of breeding adults and juveniles laying eggs in February and April and 0.6 in March.

Modelling elements:

Total female laid eggs (Table S1. – 'Difference equations').

Nº_Adults_female_laid_feb (Table S1. – 'Composed variables').

Nº_Adults_female_laid_mar (Table S1. – 'Composed variables').

Nº_Adults_female_laid_apr (Table S1. – 'Composed variables').

Nº_eggs_from_adult_feb (Table S1. – 'Composed variables').

Nº_eggs_from_adult_mar (Table S1. – 'Composed variables').

Nº_eggs_from_adult_apr (Table S1. – 'Composed variables').

Nº_Adults_female_laid_eggs_per_day_feb (Table S1. – 'Composed variables').

Nº_Adults_females_laid_eggs_per_day_mar (Table S1. – 'Composed variables').

Nº_Adults_females_laid_eggs_per_day_apr (Table S1. – 'Composed variables').

Nº_Female_Imm_laid_feb (Table S1. – 'Composed variables').

Nº_Female_Imm_laid_mar (Table S1. – 'Composed variables').

N°_Female_Imm_laid_apr (Table S1. – 'Composed variables').

N_eggs_Imm_feb (Table S1. – 'Composed variables').

N_eggs_Imm_mar (Table S1. – 'Composed variables').

N_eggs_Imm_apr (Table S1. – 'Composed variables').

N_Females_Imm_laid_eggs_per_day_feb (Table S1. – 'Composed variables').

N_Females_Imm_laid_eggs_per_day_mar (Table S1. – 'Composed variables').

*N_Females_Imm_laid_eggs_per_day_apr (*Table S1. – 'Composed variables').

Egg laying rate

We used a POISSON distribution with mean of 2.5, to adjust for the correspondent number of eggs laid per breeder female per year (Silva, 2015).

Modelling elements:

N°_eggs_per_famale_rate (Table S1. – 'Composed variables').

Eggs natural mortality

The natural mortality of eggs was assumed as random values within described limits, i.e. between 0.24 and 0.38 eggs per nest in adult birds and between 0.48 and 0.60 eggs per nest in immature birds (Neto, 1997; Silva, Luís, & Oliveira, 2017). The natural mortality of eggs was transformed into daily rates (min: 0.0072 and max: 0.0108 eggs per nest per day in adult birds; min: 0.0132 and max: 0.0158 eggs per nest per day in immature birds).

Modelling elements:

Egg_from_adult_natural_mortality_rate (Table S1. – 'Random variables').

Egg_from_adult_immature_mortality_rate (Table S1. – 'Random variables').

T_Low_egg_from_adult_mortality_rate (Table S1. – 'Constant').

T_High_egg_from_adult_mortality_rate (Table S1. – 'Constant').

T_Eggs_from_immature_low_natural_mortality_rate (Table S1. – 'Constant').

T_Eggs_from_immature_high_natural_mortality_rate (Table S1. – 'Constant').

2. ANTHROPOGENIC AND ECOLOGICAL FACTORS

Five sub-models concerning the main disturbances affecting the Berlengas shag population were considered. After modelling each disturbance independently, the result was applied to the corresponding age class of Shag population dynamics.

STATE VARIABLES

Food availability (*Sandeels scenario 0 1 2*) (Table S1. – 'Difference equations').

Temperature of February (*Temperature_Feb*) (Table S1. – 'Difference equations').

- **Bycatch mortality**

Incidental bycatch is one of the most important threats to seabirds worldwide, affecting more than 200,000 seabirds just in European waters (Genovart *et al*., 2017; Dias *et al*., 2019). Considering the mortality due to bycatch for juveniles and non-juveniles birds (i.e. on average 9% for juveniles and 3% for non-juvenile; Genovart *et al*., 2017; Velando and Freire, 2002), we applied this mortality to adults, immatures (non-juveniles) and juveniles as a normal distribution with SD of 0.1 of the average rate, after transformation into 0.00008 dead birds per day in non-juveniles and 0.00025 dead birds per day in juveniles.

Modelling elements:

Bycatch_juvenile_rate (Table S1. 'Composed variables').

Bycatch_non_juvenile_rate (Table S1. 'Composed variables').

- **Mortality due to rats**

Invasive mammals represent one the most critical problems for island ecosystems with seabird breeding colonies (Jones *et al*., 2008). In Berlengas, rats-associated mortality and nest abandonment had impacts on eggs and chicks survival, affecting 30% of Shag' nests (Silva, 2015). We calculated an averaged predation of 0.64 eggs and 0.39 chicks per nest.

These predation rates (of eggs and chicks) were used to aggravate eggs unviability and chicks mortality. For this, these rates were transformed in daily rates that ranged between absence of predation (0) and 0.0166 eggs predated by rats per day and 0.0062 chicks predated by rats per day.

Modelling elements:

Chicks_over_rat_mortality_rate (Table S1. 'Composed variables').

Egg_over_rat_mortality_rate (Table S1. 'Composed variables').

T_Eggs_over_rat_mortality_rate (Table S1. – 'Constant').

T_Chicks_over_rat_mortality_rate (Table S1. – 'Constant').

- **Adverse weather and chick mortality**

Chicks mortality is related to adverse meteorological events during May, following the regression y = 3.50x - 1.00 (R2 = 0.97) (Velando, Ortega-Ruano, & Freire, 1999), where y is the % of dead chicks and x is the number of bad weather days in May. Velando *et al*. (1999) considers bad weather when wind gusts are stronger than 29 km h-1 and daytime rainfall is over 10 mm. We have calculated the probability of adverse meteorological events using data from the last five years in the Berlengas archipelago, obtained from https://www.windguru.cz/1528 and SNIRH, National System of Information and Water Resources, http://snirh.apambiente.pt. An average annual mortality rate per bad day (0.034) was gauged and subsequently transformed in daily rates (0.001). In order to increase the realism, we applied a normally distributed chicks daily mortality rate per bad day and SD of 0.1 of the average daily rate.

Modelling elements:

Bad_days_in_May_probability_rate (Table S1. – 'Composed variables).

Bad_weather_mortality_chicks_rate_per_day (Table S1. – 'Composed variables).

T_Bad_weather_mortality_chicks_per_day_rate (Table S1. – 'Constant')

- **Tourism disturbance-associated mortality**

In the absence of direct information on the effect of the Berlengas' tourism disturbance, we assumed an impact similar to that caused by the days with adverse meteorology, which results in the lack of visibility and reduced foraging efficiency. Disturbance caused by recreational boats was defined assuming that tourists use the same areas as foraging Shags, resulting in less foraging efficiency which consequently increases chicks mortality (Velando & Munilla, 2011b). Since this effect is particularly evident during the weekends when most tourists visit the area (Silva, 2015; Fernandes, 2016), we aggravated the chicks mortality

rate using the same disturbance rate from bad weather events in all weekends of May, when tourists start visiting the island and chicks are still in nests.

Modelling elements:

Chicks_disturbance_mortality_chicks_rate (Table S1. 'Composed variables').

Probability_of_a_bad_day_in_May_and_Mortality (Table S1. 'Composed variables').

Disturbance_chick_mortality_rate (Table S1. 'Composed variables').

T_Disturbance_chick_mortality_rate (Table S1. – 'Constant').

- **Oil spill mortality**

Accidental oil spill at sea results massive seabird mortality (Troisi, Barton, & Bexton, 2016). Catastrophic oil spills were included in the model as possible occurrences, and the probability of large oil spills (> 60,000 tons) on the Atlantic coast of the Iberian Peninsula was calculated using the average occurrence of accidents since 1975 (ITOPF, 2007). This frequency (every 9 ± 7.5 years) was translated into the model as a daily probability rate (0.0003). An oil spill accident and its effect originates an immediate impact on the population that might last up to a year. Therefore, in the event of an oil spill accident, the associated mortality was applied until the following year (Martínez-Abraín *et al*., 2006). Moreover, age classes and sexes are affect in a different manner by an oil spill. When an oil spill occurs, we assume that 5% of the population dies, from which 85% are females and 65% are juveniles (Velando, Munilla, & Leyenda, 2005; Martínez-Abraín *et al*., 2006).

Modelling elements:

Oil_spill_probability_day_rate (Table S1. 'Constats').

Spill_probability_day (Table S1. 'Composed variables').

Oil_spill_juvenile_male_mortality_rate (Table S1. 'Composed variables').

Oil_spill_juvenile_female_mortality_rate (Table S1. 'Composed variables').

Oil_spill_non_juvenile_male_mortality_rate (Table S1. 'Composed variables').

Oil_spill_non_juvenile_female_mortality_rate (Table S1. 'Composed variables').

T_Oil_spill_juvenile_female_mortality_rate (Table S1. 'Constats').

T_Oil_spill_juvenile_male_mortality_rate (Table S1. 'Constats').

T_Oil_spill_non_juvenile_female_mortality_rate (Table S1. 'Constats').

T_Oil_spill_non_juvenile_male_mortality_rate (Table S1. 'Constats').

T_Oil_spill_non_juvenile_female_mortality_rate (Table S1. 'Constats').

Anthropogenic mortality for the different age classes

- **Adult anthropogenic mortality**

Daily anthropogenic mortality was determined by non-juvenile bycatch mortality rate (both sexes) of 0.00008, oil spill mortality rate of 0.002 for non-juvenile males and 0.014 for non-juvenile females.

Modelling elements:

Adult_male_antro_mortality (Table S1. – 'Process equations').

Adult_female_antro_mortality (Table S1. – 'Process equations').

Bycatch_non_juvenile_rate (Table S1. 'Composed variables').

T_Bycatch_non_juvenile_rate (Table S1. – 'Constant').

T_Oil_spill_non_juvenile_male_mortality_rate (Table S1. – 'Constant').

T_Oil_spill_non_juvenile_female_mortality_rate (Table S1. – 'Constant').

- **Immature anthropogenic mortality**

Daily anthropogenic mortality was determined by non-juvenile bycatch mortality rate of 0.00008 (both sexes), non-juvenile male (0.002) and non-juvenile female (0.014) oil spill mortality rate.

Modelling elements:

Immature_male_antro_mortality (Table S1. – 'Process equations').

Immature_female_antro_mortality (Table S1. – 'Process equations').

T_Bycatch_non_juvenile_rate (Table S1. – 'Constant').

T_Oil_spill_non_juvenile_male_mortality_rate (Table S1. – 'Constant').

T_Oil_spill_non_juvenile_female_mortality_rate (Table S1. – 'Constant').

- **Juvenile anthropogenic mortality**

Daily anthropogenic mortality was determined by incidental bycatch with a rate of 0.00025, juvenile oil spill mortality rate of (both sexes) of 0.005 for males and 0.028 for females.

Modelling elements:

Juvenile_male_ antro _mortality (Table S1. – Process equations').

Juvenile_female_ antro _mortality (Table S1. – Process equations').

T_Bycatch__juvenile_rate (Table S1. – 'Constant').

T_Oil_spill_ juvenile_male_mortality_rate (Table S1. – 'Constant').

T_Oil_spill_ juvenile_female_mortality_rate (Table S1. – 'Constant').

- **Chicks anthropogenic mortality**

Chicks were affected by rats, tourism disturbance and oil spill as anthropogenic mortality. Daily anthropogenic mortality was determined by rat-associated mortality rate of 0.006, tourism disturbance 0.001 and an oil spill mortality of 0.014 (Hall, 1979).

Modelling elements:

T_Chicks_over_rat_mortality_rate (Table S1. – 'Constant').

T_Disturbance_chick_mortality_rate (Table S1. – 'Constant').

T_Oil_spill_non_juvenile_female_mortality_rate (Table S1. – 'Constant').

- **Eggs anthropogenic mortality**

Daily anthropogenic mortality was determined by rat-associated mortality rate of 0.0167 and oil spill mortality rate of 0.014.

Modelling elements:

T_Eggs_over_rat_mortality_rate (Table S1. – 'Constant').

T_Oil_spill_non_juvenile_female_mortality_rate (Table S1. – 'Constant').

Appendix IV. Additional information on the biology and ecology of European Shag (Gulosus aristotelis)

The Iberian-Atlantic population of Shag (subsp. aristotelis) has approximately 1,390 pairs, distributed between the Galician coasts on the Spanish side (the largest population, 94% approximately) and the Portuguese coast (del Moral & Oliveira, 2019). The population trend of this subspecies in the Iberian Peninsula presents a significant decline (del Moral & Oliveira, 2019). An example of this decline is the loss of breeding pairs in Galicia (the most important reproductive nucleus), which has decreased by almost 500 pairs (26.1%) in the last 25 years (Munilla & Barros, 2019).

The Portuguese population of Shag represents a small percentage of the Iberian (circa 5.1%). According with the last Iberian breeding census, 101 pairs are estimated for Portugal, distributed within nine colonies (del Moral & Oliveira, 2019; Oliveira, 2019). The distribution of the species is quite dispersed along the Portuguese coast, occurring between Peniche and the Peninsula of Sagres. It is distributed in the southernmost coastal districts of the country, where the coast is characterized by rocky slopes (Oliveira, 2019). Between 2002 and 2017, the population in the Berlengas islands depicted a marked decline (Lecoq 2003; Pereira and Oliveira 2019). Additional data demonstrate that this trend is similar to that estimated in the last 40 years (Oliveira *et al*., 2016). This is particularly relevant since the Berlengas archipelago provides habitat for 62-75 breeding pairs in Portugal (≈60-75% of the total population) (Silva, Luís, & Oliveira, 2017; Pereira & Oliveira, 2019), classified as Vulnerable by the National Red Book (Cabral *et al*., 2005).

Like many other seabirds, Shags are long-lived birds with an average life-span of 14-15 years, while most individuals do not breed until they reach 3 years old (Del Hoyo *et al*., 2018). Appart from the previous information, a proportion of immature individuals (47% of juvenile females) was simulated to breed in their second year of life, accordingly with Velando and Freire (2002). Although nests are built on the edges of rocky cliffs or in the resulting hollows of the rugged coastline, protected from the sea and rain, this factor was not considered limitative for the breeding population in the model, due to the favourable geomorphological conditions presented by the BSPA (Potts *et al*., 1980; Snow, 1963; Silva *et al*., 2015). Regarding the date of the first laying, we have assumed in the model the average BSPA schedule: nest are occupied during January and the eggs hatch from the end of March

to the beginning of June (Neto, 1997; Silva, 2015). One month in average for the incubation and a breeding success of around 1.3 were also simulated (Cramp & Simmons, 1977; Silva, Luís, & Oliveira, 2017). On the other hand, the number of eggs laid by each female per breeding season was defined as following a Poisson distribution with a mean of 2.5 (Velando & Freire, 2002; Silva, 2015).

Onshore and offshore factors affect the species, including environmental stochasticity and ongoing anthropogenic activities (Croxall *et al*., 2012) (Table 1, main document). The most significant stressors, considered key-factors are described in the main part of this paper: invasive mammals, bycatch from different fishing gears (mainly gillnets), extreme climatic events, tourist activities and oil spill events. However, we also studied the possibility of incorporating other effects into the model such as interspecific competition for nesting places and competition with kleptoparasites such as seagulls (Velando & Freire, 2002; Dias *et al*., 2019) or the fishing fleet impact (Dias *et al*., 2019). Nonetheless, interspecific and intraspecific competition seem to have no significant effects in the breeding success of the BSPA population (Fagundes, Oliveira, & Andrade, 2017). On the other hand, since sandeels (the main prey of Shags in the study area), have low commercial value in Iberia (R. Furness & Tasker, 2000; DGRM, 2019), we have assumed in the model simulations no mortality associated with fishermen competition.

Table S1. Supplementary references consulted for model conceptualization and calibration

Important information consulted	Reference
Changes in Shag population	(Aebischer, 1986)
Human disturbances and burrow nesting birds	(Albores-Barajas, Soldatini, & Furness, 2009)
Birds populations in Portugal	(Hany Alonso *et al.*, 2019)
Effects of longlines bycatch on seabirds	(Anderson *et al.*, 2011)
Diet of different species of 'cormorants'	(Barrett *et al.*, 1990)
Effects of research disturbance on seabirds	(Blackmer, Ackerman, & Nevitt, 2004)
Procellariformes recovery after rat eradication	(Borrelle *et al.*, 2018)
Dynamic modelling	(Buchadas *et al.*, 2017)
Seabird colony changes after rat eradication	(Buxton *et al.*, 2016)
Effects of oil on seabirds	(Camphuysen & Leopold, 2004)
Review of human disturbances on seabirds	(Carney & Sydeman, 1999)
Effects of oil on seabirds: Case of Prestige	(Castege *et al.*, 2007)
Identifying ecological indicators	(Dale & Beyeler, 2001)
Impact of climate on seabirds	(Daunt & Mitchell, 2013)
Seabirds as ecological indicator	(Diamond & Devlin, 2003)
Modelling system dynamics	(Flores *et al.*, 2014)
Shag population ecology	(Fortin *et al.*, 2013)
Longevity European bids	(Fransson *et al.*, 2010)
Relative impact of hunting and oiling on Guillemots	(Frederiksen *et al.*, 2019)
Effects of oil on seabirds feathers	(Fritt-Rasmussen *et al.*, 2016)
Interactions between sandeels fishing and seabirds	(R. W. Furness, 2002)
Seabirds population viability under fishing management scenarios	(Genovart *et al.*, 2017)
Effects of human disturbance on penguin behavior	(Giese, 1996)
Performance assessment to mitigate longlines bycatch on seabirds	(Gilman, Boggs, & Brothers, 2003)
Productivity of coral reefs without invasive rats	(Graham *et al.*, 2018)
Management and conservation planning	(Grantham *et al.*, 2010)
Dynamic modelling	(Hazen *et al.*, 2017)
Predation of eggs by Yellow-legged gull	(Hernández-Matías & Ruiz, 2003)

Table S1. (Cont.)

Important information consulted	Reference
Diet of Shag	(Johnstone *et al.*, 1990)
Ecological Indicators for Assessment of Ecosystem Health	(Jorgensen, Xu, & Costanza, 2016)
Protected areas guidelines	(Kelleher, 1999)
Ecosystem recovery after rat eradication	(Le Corre *et al.*, 2015)
Seabird conservation management	(Lewison *et al.*, 2012)
Fishing interactions with Shag in Berlengas	(Lopes, 2018)
Shag feeding behavior	(Lumsden & Haddow, 1946)
Tourism disturbance on seabirds	(Marcella *et al.*, 2017)
Effects of disturbance on seabirds	(Martínez-Abraín *et al.*, 2008)
Effects of oil on seabirds: Exxon Valdez	(Piatt *et al.*, 1990)
Seabirds as bioindicators	(Rajpar *et al.*, 2018)
Breeding success and sandeels abundance	(Rindorf, Wanless, & Harris, 2000)
Rat invasion pathway	(Robins *et al.*, 2016)
Invasive mammals on Mediterranean islands	(Ruffino *et al.*, 2009)
Comments to umbrella species criteria	(Seddon & Leech, 2008)
Seabirds population conservation	(Shaffer, 1981)
Seabirds biology	(Shreiber & Burger, 2001)
Island management and causes of extinction	(Simberloff, 2000)
Shag population ecology	(Velando, 1997)
Shag foraging behaviour	(Wanless, Harris, & Morris, 1991)
Human disturbances reduce reproduction of seabird	(Watson, Bolton, & Monaghan, 2014)
Modelling system dynamics	(Weller *et al.*, 2014)
Effects of human disturbance on penguin behavior	(Yorio & Boersma, 1992)
Global review of seabirds bycatch	(Žydelis, Small, & French, 2013)

Appendix V. Effect size comparison results (Cohen's d), generalized linear model (GLzM), post-hoc comparisons for pairwise of all scenarios and one-parameter-at-a-time technique (OAT) sensitivity analysis.

Table S3. Effect size comparison, between all scenarios except with the baseline (depicted in table 3), of the results simulated for the period considered. Cohen's d estimate, effect sizes using Cohen estimator; lower and upper 95% CI represents 95 percent confidence interval, and Interpretation shows the magnitude of Shag population change between scenarios compared. 1: baseline scenario (scenario 1); scenario 2: no bycatch; scenario 3: no rats; scenario 4: no tourist disturbances; scenario 5: no rats, no bycatch; scenario 6: no rats, no tourist disturbances; scenario 7: no bycatch, no tourist disturbances and scenario 8: no rats, no accidental capture, no tourist disturbance.

Pairwise scenarios	Cohen's d estimate	lower 95% CI	upper 95% CI	Interpretation
2:03	2.86	3.26	2.46	**large**
2:04	-2.75	-3.14	-2.36	**large**
2:05	5.71	5.08	6.34	**large**
2:06	3.16	2.74	3.58	**large**
2:07	-0.05	-0.33	0.23	**negligible**
2:08	5.35	4.75	5.95	**large**
3:04	-4.87	-5.43	-4.32	**large**
3:05	2.75	2.37	3.14	**large**
3:06	0.14	-0.14	0.42	**negligible**
3:07	-2.95	-3.35	-2.55	**large**
3:08	2.71	2.33	3.1	**large**
4:05	7.48	6.69	8.26	**large**
4:06	5.27	4.68	5.86	**large**
4:07	2.80	2.40	3.19	**large**
4:08	6.95	6.21	7.69	**large**
5:06	-2.70	-3.09	-2.32	**large**
5:07	-5.82	-6.46	-5.18	**large**
5:08	0.15	-0.13	0.43	**negligible**
6:07	-3.26	-3.69	-2.84	**large**
6:08	2.66	2.28	3.04	**large**
7:08	5.44	4.83	6.04	**large**

Table S4. Results of the generalized linear model (GLzM) to evaluate the divergence between the baseline scenario (scenario 1) and all other scenarios. Scenario 2: no bycatch; scenario 3: no rats; scenario 4: no tourism disturbance; scenario 5: no rats, no bycatch; scenario 6: no rats, no tourism disturbance; scenario 7: no bycatch, no tourism disturbance and scenario 8: no rats, no bycatch, no tourism disturbance.

Scenarios	Estimate	Std. Error	t value	Pr(>|t|)
2_no bycatch	11.54	0.53	21.90	<0.001
3_no rats	20.77	0.54	38.24	<0.001
4_no disturbance	1.30	0.51	2.55	0.01
5_no rats, no bycatch	37.00	0.57	64.88	<0.001
6_no rats, no disturbance	21.30	0.54	39.16	<0.001
7_no bycatch, no disturbance	11.71	0.53	22.21	<0.001
8_no rats, no bycatch, no disturbance	37.73	0.57	66.02	<0.001

Table S5. Medians, p-values and t coefficient (Steel-Dwass Test) for pairwise comparisons of all scenarios considered for the Berlengas Shag population. 1st and 2nd are the median number of Shags after 10 years of simulation for the respective scenarios. Shaded values depict no significant difference.

Pairwise scenarios	Adult female				Juvenile female			
	1st comparative scenario median	2nd comparative scenario median	t	p-value	1st comparative scenario median	2nd comparative scenario median	t	p-value
1:02	65.49	83.14	36.08	<0.001	25.52	27.58	17.90	<0.001
1:03	65.49	105.67	34.67	<0.001	25.52	44.20	34.22	<0.001
1:04	65.49	67.51	5.57	<0.001	25.52	26.13	4.22	0.00
1:05	65.49	134.59	37.89	<0.001	25.52	50.06	35.68	<0.001
1:06	65.49	106.92	34.47	<0.001	25.52	46.48	34.20	<0.001
1:07	65.49	82.85	36.30	<0.001	25.52	27.75	18.43	<0.001
1:08	65.49	136.37	37.79	<0.001	25.52	52.05	35.53	<0.001
2:03	83.14	105.67	14.79	<0.001	27.58	44.20	33.72	<0.001
2:04	83.14	67.51	33.65	<0.001	27.58	26.13	15.16	<0.001
2:05	83.14	134.59	25.34	<0.001	27.58	50.06	34.80	<0.001
2:06	83.14	106.92	15.14	<0.001	27.58	46.48	33.72	<0.001
2:07	83.14	82.85	0.32	1	27.58	27.75	0.98	0.98
2:08	83.14	136.37	24.62	<0.001	27.58	52.05	34.45	<0.001
3:04	105.67	67.51	32.89	<0.001	44.20	26.13	34.02	<0.001
3:05	105.67	134.59	16.76	<0.001	44.20	50.06	14.85	<0.001
3:06	105.67	106.92	0.74	0.10	44.20	46.48	2.6	0.16
3:07	105.67	82.85	14.42	<0.001	44.20	27.75	33.70	<0.001
3:08	105.67	136.37	16.78	<0.001	44.20	52.05	16.96	<0.001
4:05	67.51	134.59	37.09	<0.001	26.13	50.06	35.42	<0.001
4:06	67.51	106.92	32.72	<0.001	26.13	46.48	33.98	<0.001
4:07	67.51	82.85	33.93	<0.001	26.13	27.75	15.85	<0.001
4:08	67.51	136.37	36.94	<0.001	26.13	52.05	35.22	<0.001
5:06	134.59	106.92	16.26	<0.001	50.06	46.48	12.66	<0.001
5:07	134.59	82.85	25.10	<0.001	50.06	27.75	34.77	<0.001
5:08	134.59	136.37	0.59	0.10	50.06	52.05	3.16	0.03
6:07	106.92	82.85	14.78	<0.001	46.48	27.75	33.71	<0.001
6:08	106.92	136.37	16.31	<0.001	46.48	52.05	14.96	<0.001
7:08	82.85	136.37	24.41	<0.001	27.75	52.05	34.41	<0.001

Table S6. Local sensitivity analysis (one-parameter-at-a-time) of the main state variables of the model to +/– 10% and +/–50% variation of the parameter values.

Parameter	Sensivity	Adults female	Adults male	Eggs from adults	Eggs from immatures	Chicks from adults	Chicks from immatures	Juveniles female	Juveniles male	Immatures female	Immatures male
Adult mortality	-50	-1.23	-1.23	-0.76	0.04	0.05	0.00	0.05	0.04	-0.03	-0.03
	-10	-0.84	-0.85	-0.94	-0.75	0.19	-0.69	0.08	0.03	-0.6	-0.55
	10	-1.65	-1.64	-1.39	0.47	-0.70	0.58	-0.19	-0.13	0.81	0.84
	50	-0.58	-0.59	-0.45	-0.02	-0.16	0.01	-0.08	-0.08	0.13	0.13
Eggs from adult mortality	-50	-0.30	-0.30	-0.41	-0.01	-0.55	0.01	-0.34	-0.35	-0.19	-0.20
	-10	-0.49	-0.43	-0.85	-0.33	0.17	-0.37	-0.02	-0.03	-1.23	-1.22
	10	-0.91	-0.96	-0.50	-0.11	-0.77	-0.01	-0.26	-0.21	0.43	0.45
	50	-0.25	-0.25	-0.23	-0.17	-0.34	-0.11	-0.24	-0.24	-0.04	-0.04
Eggs from immature mortality	-50	-0.02	-0.01	-0.07	-0.41	0.11	-0.46	-0.10	-0.12	-0.40	-0.40
	-10	0.39	0.38	-0.30	0.36	-0.04	0.24	1.10	1.03	0.13	0.09
	10	-0.29	-0.33	-0.22	0.39	-0.06	0.35	0.03	0.05	0.69	0.56
	50	-0.11	-0.11	0.02	-0.09	0.03	-0.12	-0.17	-0.16	0.02	0.02
Chicks from adults mortality	-50	-0.01	-0.02	-0.09	0.14	0.03	0.12	0.06	0.06	0.06	0.06
	-10	-0.17	-0.11	-0.41	-1.03	-0.12	-0.90	-0.40	-0.47	-1.05	-1.12
	10	-0.65	-0.62	-0.69	-0.62	-0.73	-0.46	-0.81	-0.77	-0.49	-0.64
	50	-0.25	-0.25	-0.29	-0.27	-0.19	-0.24	-0.40	-0.39	-0.29	-0.26
Chicks from immature mortality	-50	-0.10	-0.09	-0.27	-0.26	0.08	-0.26	-0.01	-0.03	-0.30	-0.31
	-10	-0.37	-0.28	0.59	-0.74	0.73	-0.77	0.22	0.18	-1.46	-1.37
	10	0.16	0.15	0.87	1.22	-0.50	1.01	0.04	0.11	1.90	1.87
	50	0.03	0.02	0.00	0.11	-0.08	0.08	0	0.01	0.14	0.14
Juvenile mortality	-50	-0.39	-0.37	-0.22	-0.70	-0.02	-0.56	-0.31	-0.32	-0.75	-0.75
	-10	-0.24	-0.22	-0.41	0.13	0.28	0.11	0.46	0.43	-0.3	-0.29
	10	-0.51	-0.57	-1.24	0.37	-0.37	0.36	-0.37	-0.31	0.50	0.49
	50	-0.36	-0.36	-0.21	-0.28	-0.06	-0.22	-0.37	-0.36	-0.28	-0.28
Immature mortality	-50	-0.18	-0.18	-0.34	-0.03	0.03	-0.04	-0.03	-0.04	-0.24	-0.24
	-10	-0.38	-0.27	-1.19	0.71	-0.39	0.65	0.20	0.16	-0.43	-0.41
	10	-0.47	-0.52	-0.81	-0.07	-0.64	0.09	-0.45	-0.39	-0.20	-0.20
	50	-0.17	-0.18	-0.31	0.18	-0.09	0.17	-0.01	0.00	0.09	0.09
Number of laid eggs	-50	0.56	0.56	1.10	1.20	0.68	1.11	0.93	0.93	0.61	0.60
	-10	0.53	0.44	0.96	1.31	0.73	1.12	2.77	2.74	0.51	0.44
	10	0.24	0.19	1.34	0.83	-0.01	0.72	-0.00	0.03	0.36	0.33
	50	0.19	0.18	0.91	1.32	0.14	1	0.30	0.30	0.46	0.46

Table S6. (Cont.)

Parameter	Sensivity	Adults female	Adults male	Eggs from adults	Eggs from immatures	Chicks from adults	Chicks from immatures	Juveniles female	Juveniles male	Immatures female	Immatures male
General bycatch	-50	-0.27	-0.25	-0.46	-0.27	0.03	-0.24	0.13	0.12	-0.27	-0.28
	-10	-0.45	-0.43	0.21	-1.13	0.29	-0.98	-0.19	-0.23	-1.39	-1.41
	10	-0.81	-0.79	-0.41	-0.59	0.01	-0.45	-1.30	-1.24	-0.47	-0.42
	50	-0.08	-0.08	-0.05	0.2	-0.08	0.17	-0.05	-0.04	0.18	0.16
Juvenile bycatch	-50	-0.07	-0.05	-0.15	-0.27	0.07	-0.22	-0.02	-0.04	-0.37	-0.38
	-10	-0.14	-0.13	-0.70	-0.99	-0.55	-0.95	-0.58	-0.62	-1.45	-1.51
	10	0.08	0.03	0.95	0.50	-0.34	0.41	-0.16	-0.11	0.71	0.76
	50	-0.04	-0.05	0.04	0.16	-0.08	0.14	-0.21	-0.20	0.25	0.24
Non-juvenile bycatch	-50	-0.26	-0.24	0.02	-0.24	0.03	-0.23	-0.05	-0.06	-0.32	-0.33
	-10	-0.28	-0.22	-0.41	-1.50	0.16	-1.23	-0.24	-0.31	-1.54	-1.54
	10	-0.25	-0.24	-0.00	1.04	-0.16	1.04	0.30	0.31	1.53	1.52
	50	-0.1	-0.11	-0.01	0.16	-0.02	0.16	0.08	0.09	0.24	0.25
Eggs predation by rats	-50	-0.24	-0.25	-0.49	-0.03	-0.48	-0.06	-0.05	-0.06	-0.03	-0.05
	-10	-0.44	-0.40	0.16	-0.83	-0.33	-0.82	-0.34	-0.43	-1.21	-1.18
	10	-0.51	-0.52	-0.03	0.67	-0.81	0.59	-2.06	-2.00	0.79	0.88
	50	-0.22	-0.22	-0.40	-0.28	-0.30	-0.27	-0.35	-0.34	-0.32	-0.31
Chick predation by rats	-50	-0.09	0.10	0.11	0.09	0.03	0.06	0.00	-0.00	-0.09	-0.10
	-10	0.48	0.45	0.24	0.03	0.36	0.03	0.22	0.18	-0.25	-0.21
	10	0.26	0.31	0.37	1.05	0.67	0.82	-0.16	-0.10	1.41	1.47
	50	-0.05	0.06	0.05	0.25	0.11	0.17	-0.14	-0.13	0.17	0.18
Disturbance chicks mortality	-50	-0.01	0.00	0.04	-0.10	0.02	-0.08	-0.02	-0.03	-0.10	-0.09
	-10	-0.19	0.22	0.28	-1.19	0.19	-0.99	-0.24	-0.28	-0.93	-0.97
	10	0.5	0.46	1.63	1.48	0.38	1.31	0.12	0.15	0.10	0.95
	50	0.03	0.01	0.05	0.15	0.15	0.12	-0.07	-0.07	0.24	0.24
Bad weather chicks mortality	-50	0.11	0.11	0.07	0.07	0.01	0.06	0.03	0.02	0.05	0.05
	-10	0.43	0.45	0.44	1.32	0.50	1.11	2.46	2.42	1.04	0.10
	10	0.41	0.36	1.60	1.17	0.49	0.98	-0.82	-0.81	1.25	1.33
	50	-0.1	0.11	0.25	0.06	0.08	0.07	-0.01	0	0.14	0.15
Juvenile males oil spill mortality	-50	0.03	0.04	0.22	-0.02	0.13	-0.01	0.08	0.06	-0.04	-0.04
	-10	-0.37	0.34	0.10	-0.72	0.7	-0.68	0.10	0.02	-1.26	-1.27
	10	-0.25	0.30	0.47	1.03	0.05	0.96	0.32	0.40	0.96	1.01
	50	-0.03	0.04	0.05	0.32	0.01	0.28	0.06	0.07	0.27	0.3

Table S6. (Cont.)

Parameter	Sensivity	Adults female	Adults male	Eggs from adults	Eggs from immatures	Chicks from adults	Chicks from immatures	Juveniles female	Juveniles male	Immatures female	Immatures male
Juvenile females oil spill mortality	-50	0.01	0.02	0.12	-0.20	0.12	-0.17	0.03	0.03	-0.25	-0.25
	-10	0.01	0.01	0.20	0.19	0.06	0.08	0.65	0.59	-0.88	-0.94
	10	0.32	0.27	0.01	0.37	0.12	0.26	-1.08	-0.10	0.60	0.63
	50	0.10	0.08	0.18	0.23	0.08	0.20	0.03	0.04	0.31	0.32
Non-juvenile males oil spill mortality	-50	0.01	0.02	0.14	-0.13	0.06	-0.13	0.11	0.10	-0.18	-0.17
	-10	-0.05	0.00	0.59	-0.50	0.41	-0.52	0.52	0.5	-0.19	-0.24
	10	0.19	0.13	0.78	-1.20	0.44	-1.08	-0.83	-0.75	-0.75	-0.75
	50	-0.08	0.08	0.26	-0.19	-0.08	-0.15	-0.05	-0.04	-0.06	-0.05
Non-juvenile females oil spill mortality	-50	-0.05	0.04	0.03	-0.38	-0.01	-0.33	-0.08	-0.09	-0.37	-0.36
	-10	0.12	0.17	0.20	0.10	0.27	0.15	1.31	1.27	0.22	0.18
	10	0.09	0.09	-1.48	0.02	-0.81	-0.04	-1.41	-1.40	0.49	0.51
	50	0.04	0.02	0.13	0.15	0.03	0.14	0.07	0.07	0.30	0.30

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AGRADECIMIENTOS

Creo que fue en octubre de 2005 cuando me propusieron ir a la Isla de Tarifa.
«Están ahí los de la UCA censando aves marinas», me dijeron.
«¡Ostras!, pues yo quiero aprender», pensé.

Hasta entonces no me había dedicado a mirar al mar con cierta intención, así que a la isla fui. Allí estaban Gonzalo Muñoz junto a David Cuenca contando *caldios al oeste* y *morbas al este*. Dieciséis años después sigo agradeciéndote, Gonzalo, que hayas sido mi mentor, mi jefe, mi tutor, mi director de tesis y mi amigo. Gracias de corazón.

Gracias también a la Universidad de Cádiz y al grupo de investigación Conservación de Humedales Costeros por ofrecerme el paraguas y la ayuda logística ante el desafío de hacer una tesis sin beca.

Esta tesis tampoco hubiera tenido lugar sin la colaboración del Instituto Español de Oceanografía, de sus campañas ECOCADIZ, de todo el personal científico (ante el cual me quito el sombrero), de toda la tripulación del Miguel Oliver y, por supuesto, de su jefe de campaña, Fernando Ramos (Fernin), quien siempre tuvo un lugar para nosotros.

Gracias a todos los demás observadores de aves que iniciaron la toma de datos hace ya muchos años. Me gusta pensar que nuestro esfuerzo no se queda en una libreta o un cajón y que las preciosas horas en la cubierta del barco ven la luz en los capítulos de esta tesis.

La mención internacional de la tesis exige irse de estancia y la mía fue inolvidable. Dos cortos, pero intensos meses con Juan Ramírez y Gabriel Caucal en el cuerno de África bajo la batuta de Evan Buechley de la Universidad de Utah y HawkWatch International (¡thanks Evan! ¡thanks Tempe!) y otros dos productivos meses en la Universidad de Trás-os-Montes e Alto Douro UTAD en Vila Real (Portugal).

Gracias a todos los compañeros de la UTAD, en especial a Joao Alexandre Cabral por aceptarme en el laboratorio de Ecología Aplicada y, por supuesto, a mi tutor Mário Santos, quien con paciencia extrema y una capacidad de trabajo fuera de lo común, sacó tantos ratos como fue necesario para que juntos, 'salváramos' a la Galheta. Gracias Mário.

Mil gracias a Rita, Teresa, Marisa, Luis, Nazaret, Hélia, Virginia, Fátima, Thayanne y Paulo. Obrigado aos meus colegas de Vila Real, por me ajudarem a entender a língua Portuguesa e me mostrarem todos os cantinhos gastronómicos desse "Polo Norte" Português.

Lástima que mi compi de doctorado, Mar Salguero, se resbalara con el suavizante de esa lavadora y tuviera que posponer su estancia en la UTAD... muchas gracias por el contacto, Mar. Hubiera sido genial que coincidiéramos allí. Prepárate, los primeros días no te vas a enterar de nada, pero con esta gente, lo tendrás todo de cara, ya verás. Eso sí, no vayas en invierno.

Quiero agradecer la ayuda y colaboración del equipo de aves marinas de SEO/BirdLife, y en particular a Pep Arcos y Juan Bécares, quienes desde un inicio, aportaron su experiencia a esta historia.

Gracias a Darío Delgado por estar siempre dispuesto a echarme una mano con el SIG y por ese clarividente modo de entender las líneas de código.

Le agradezco de igual manera su aportación y experiencia a los otros co-autores de los artículos de esta tesis, Gabriel Navarro, Andrés Cózar, Jorge Tornero, Margarita Rincón, Mª Paz Jiménez, Rita Bastos y Elisabete Silva. ¡Quisiera ser tan listo como vosotros!

Muchas gracias a Jose Oviedo y Macarena Castro por sus consejos y ánimos en las últimas etapas de esta tesis... mucho antes deberían haber llegado vuestros consejos, ¡gracias!

De la misma manera, gracias a Elisa Martí y Sara Haro, vuestra experiencia como recién doctoradas me ha ayudado enormemente en estas últimas semanas. Muchas gracias Eli por ese decálogo de burocracia pre-tesis y la ayuda en la maquetación.

Many thanks to my English-speaking friends (Andy Paterson, Charles Wheaton and Chris Mills) for correcting my English mistakes, which are many. Thank you guys!

Fuera del ámbito académico existe una ristra enorme de gente que me ha ayudado, de una u otra manera, a finalizar este trabajo. Perdonadme si alguno se queda en el tintero.

Gracias a 'er Juan' por ser mi guía de aves de cabecera, por compartir conmigo su conocimiento ornitológico y por tantas jornadas de campo y risas. Gracias a Rafa por su apoyo, por verlo todo siempre tan fácil y por esos apuntes de Indesign. Gracias Torralvo por preguntar, por estar pendiente de mí y de los míos.

Muchas gracias a Noelia por su empujón inicial. Cuando te dije 'voy a hacer la tesis, ¿qué te parece?' Tus ánimos después de saber el esfuerzo que le dedicaste a la tuya significaron mucho.

Gracias a Currito por decir que sí a leerte este trabajo antes que ninguno y por tu positividad, que lástima que no nos veamos más.

Mil gracias a Estrella e Ibone, vuestras revisiones han mejorado mucho la lectura de esta tesis. Vaya rapidez y disposición a ayudar, chapó. En breve cambiamos los vermuts compartidos tras la pantalla por otros cara a cara.

Gracias a todos mis amigos, que tengo la suerte de tener muchos, gracias a mis amigos de Tarifa y a mis amigos de El Puerto, pero entre todos, gracias especialmente a Carlos por ayudarme en todo, por echarme una mano en cada cosa que me hacía falta sin dudar un segundo, gracias Charlie.

Y finalmente, pero no por ello menos importante, el mayor de mis agradecimientos se lo debo a mi familia. Durante este tiempo todo ha sido mucho más fácil gracias al apoyo y al cariño incondicional de mi padre y de mi madre. Desde el día que les dije que quería estudiar Biología y, sin estar totalmente convencidos, me apoyaron plenamente, hasta la repetida frase de mi madre cuando no tiene opinión ante mis inquietudes, «Yo de eso no entiendo, pero si tú crees que para ti es bueno, adelante». MIL GRACIAS.

Mª Carmen, Chiqui, muchas gracias por estar tan pendientes de mí, por estar siempre ahí, por ser tan fuertes y poder contar con vosotras para todo.

Gracias Fran, por ayudarme en cada mudanza y consejo informático y compartir conmigo la '*carga informática de mi padre*'.

Gracias a mis bombones, Lunita y Daniel, por su bondad y su alegría.

Gracias Carmen, *mi Carmen*, por el amor y la alegría que desprendes y que me das, por cada viaje juntos y por los que quedan, por cada baile de viernes. Gracias por tu paciencia en estos años de barco, de carretera, de eternas horas delante del ordenador. Gracias por tu complicidad, confianza y apoyo, me hacen sentir más grande y saber que, contigo, todo va a salir bien.

No me olvido de *perrito*, quién me obliga a levantarme de la silla y pasear y que es todo un ejemplo de cómo ser feliz.

Gracias a los pájaros, que comparten conmigo su libertad.

Muchas gracias, os quiero mucho a todos.

Notas:

Ante la preocupante situación y deterioro del medio marino, esta tesis analiza diferentes casos de estudio en el marco de las Áreas Marinas Protegidas (AMP) del arco ibérico atlántico.

Los resultados y conclusiones obtenidos en los trabajos desarrollados en estas páginas tienen el objetivo de ser una herramienta práctica que ayude a gestores en la toma de decisiones para conseguir una efectiva gestión y conservación del mar.

Para ello se han aplicado diferentes técnicas de modelado espacial y análisis demográficos a series temporales de especies indicadoras del medio, las aves marinas.

Los resultados indican que la Zona de Especial Protección para las Ave (ZEPA) del Golfo de Cádiz no cubre el área clave de especies prioritarias por las que fue declarada, como la pardela balear. De la misma manera, la distribución de esta especie en el área de estudio no se encuentra determinada por factores ampliamente aceptados en otras zonas como la clorofila, sino que, factores abióticos y la distribución de sus presas resultaron ser mejores predictores de la ocurrencia de esta y otras especies de aves marinas.

Los modelos aplicados a la población de cormorán moñudo en la ZEPA de las Islas Berlengas señalan a las ratas y al *bycatch* como las principales amenazas del cormorán. Sin aplicar ninguna medida de gestión, esta población descendería un 7% en la próxima década. No obstante, si se mantiene el archipiélago libre de carnívoros invasores y se aplican medidas de reducción de las capturas accidentales, esta población aumentaría notablemente.

Los resultados de esta tesis demuestran que las AMP estudiadas presentan notables limitaciones y no protegen eficazmente a las especies por las que fueron declaradas y, por tanto, es necesario aplicar planes de gestión reales que garanticen la conservación de las zonas marinas prioritarias.

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